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A Study of the Winter Feeding
Ecology and Behaviour
of the Bar-tailed Godwit
(*Limosa lapponica*)

by

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ABSTRACT

Godwits, large wading birds, were studied at Holy Island, Northumberland during three winters. Most fed on the polychaete worms Scoloplos armiger and Arenicola marina (the lugworm). Although 60% of items taken were Scoloplos, the larger lugworms provided over 90% of the energy content of the diet. In October and April, godwits obtained almost all their daily energy requirements during daylight hours. In December they had to feed also by night, particularly during cold weather. At sand temperatures above 3°C, godwits obtained the same amount of food each minute in mid-winter as in October; they fed for longer when their energy requirements were greater. At sand temperatures below 0°C, godwits were not able to feed fast enough to meet their requirements and had to utilize some of their fat reserves, which were sufficient to balance three days' total starvation. By comparison with captive godwits, it was concluded that wild birds expend almost as much energy in capturing worms as they require just to keep alive.

Godwits normally feed in flocks containing both males and females. The short-billed smaller males tend to feed at the tide-line, and the longer-billed larger females in deeper water. If males are forced into deeper water, they are less successful in feeding than females. Birds feeding alone are less successful than individuals within flocks, and are more likely to be caught by birds-of-prey.

Godwits feed where the availability of their prey is highest. They rely on cast-formation (defaecation) to detect lugworms, which normally live too deep to be reached by the bird's beak. Lugworms form casts most frequently at the tide-edge and less often as the sand dries out during low

tide. Hence birds move with the tide-line to feed. At temperatures below $3^{\circ}C$, lugworms defaecate most frequently in shallow water at the tide-edge, and godwits feed further into the water. Flocks change shape to become linear. Other birds are forced to feed at the tide-edge in cold weather, so godwits have to pack more closely and interactions increase. Potential feeding time is lost in fighting. Consequently, less food is obtained each minute than expected solely from the reduction in prey availability. At very low temperatures, godwits are forced to feed on Scoloplos, by touch. Females then gain an advantage from their longer legs and bills, since they can feed in deeper water and avoid the fights which are chiefly at the tide-edge.

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GENERAL INTRODUCTION

The Bar-tailed Godwit Limosa lapponica is a large wading bird which breeds in Siberia. Those from the eastern parts of the breeding range winter in Australasia, and those from western Siberia winter in West Africa and on the western seaboard of Europe. Many winter on the coasts of the British Isles, particularly on extensive areas of sandflats. In north America, the Bar-tailed Godwit is replaced by the Hudsonian Godwit Limosa haemastica, which also breeds on the tundra.

The studies described in this thesis were prompted by an interest in the extreme sexual dimorphism exhibited by godwits, particularly in bill-length. During early attempts to quantify any differences in feeding behaviour between males and females, it became clear that they were feeding on a very restricted range of prey. This presented an opportunity to make a detailed study of the way in which the behaviour of the invertebrate prey influenced the feeding behaviour of the godwit predators, and to attempt measurements of the daily food intake of the birds in the natural winter situation.

The thesis is presented as two papers (which, it is hoped, may be suitable for publication without major alteration) and three appendices. The first two of the latter contain material which is not as complete as would be desirable; the third is the manuscript of a paper which is to appear later this year (1975) in 'Wildfowl'. This paper, although largely the work of Dr. Evans, incorporates some of my observations on godwit feeding behaviour, and was based on body composition analysis of birds which I collected. It is included here chiefly because it contains information to which reference is made several times in the main sections of the thesis, and it is unlikely to be available in published form before the thesis is examined. All three Appendices are relevant chiefly to the main paper on winter feeding ecology.

The Winter Feeding Ecology of the Bar-tailed Godwit

I INTRODUCTION

Although the ornithological literature contains plenty of casual records of the foods of wading birds, not until recently have any quantitative studies been published of shorebird diets. Among the most reliable of these have been the work of Goss-Custard (1969) on Redshank *Tringa totanus*, of Heppleston (1971) on Oystercatchers *Haematopus ostralegus*, and of Prater (1972) on Knot *Calidris canutus*. The last of these was based primarily on the analysis of gizzard contents, a method which has severe limitations if many soft-bodied prey feature in the diet, since they are broken up quickly as soon as they reach the stomach. For this reason, the study reported here on the diet of the Bar-tailed Godwit *Limosa lapponica* at Lindisfarne, Northumberland, relies heavily on direct observations in the field of prey taken. As will be shown, most of these are marine worms, which leave few distinguishable remains in the gizzard, particularly the lugworm *Arenicola marina*.

Field observations also allowed measurement of the amount of food eaten by godwits during daylight hours in the wild. Such estimates exist for very few carnivorous birds, except those held in captivity, and it will be shown that the energy expended in obtaining food in the natural situation is almost equivalent to that needed for godwits to stay alive and healthy in captivity at equivalent temperatures.

Finally, this study shows how even a quantitative description of a predator's diet is of little value unless related to the variety, density and availability of potential prey in the area.

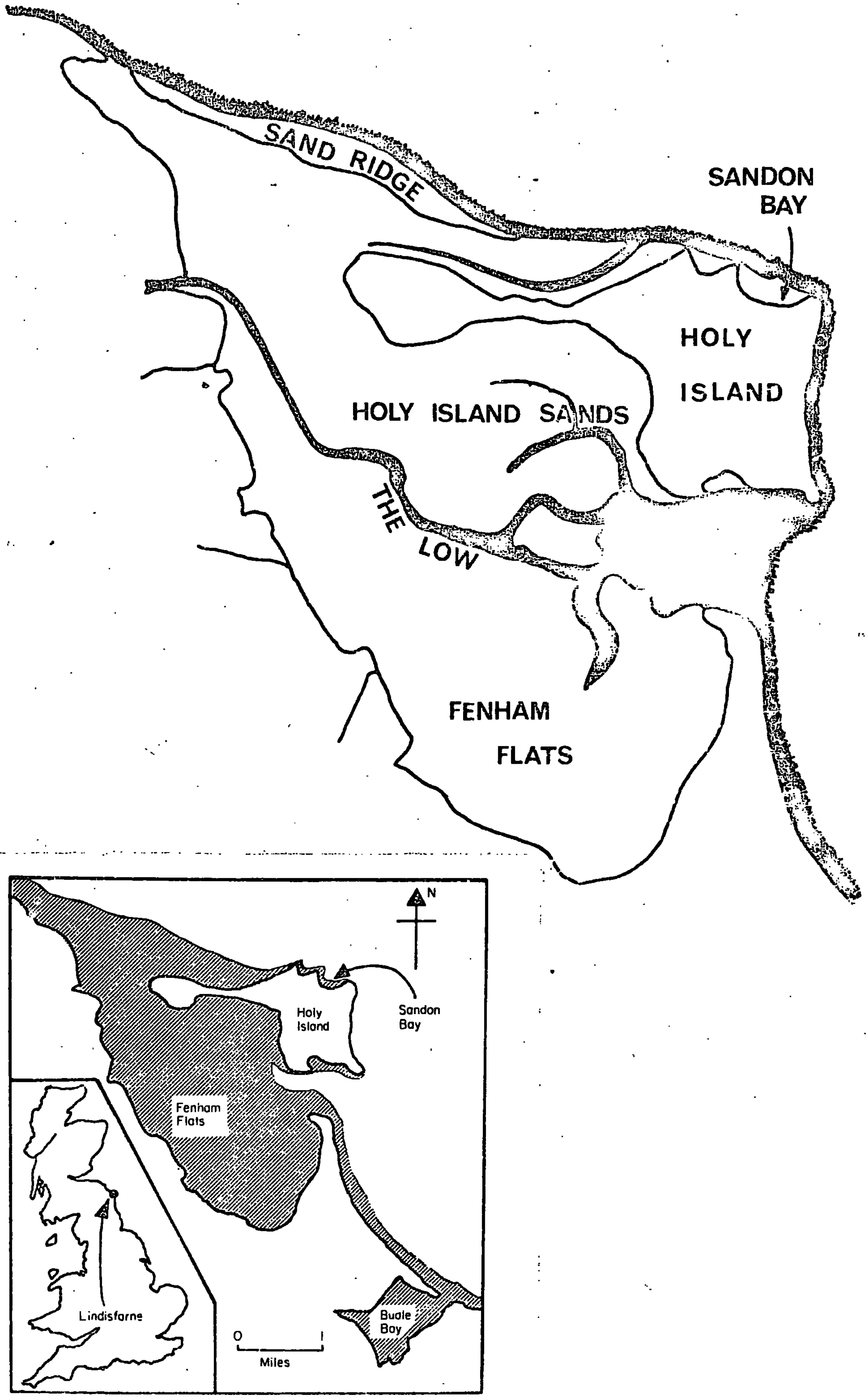

Fig. 1 The intertidal sand and mud-flats at Lindisfarne, Northumberland

II STUDY AREA

The Lindisfarne National Nature Reserve in north Northumberland comprises about 3240 hectares (12½ square miles), mainly of tidal mud and sand-flats, saltmarsh and dunes.

My research was located on the largest area of mud and sand-flats, which are partially enclosed between Holy Island and the mainland (Fig. 1). The main channel draining this area divides approximately 1100 hectares on the mainland side (chiefly of mudflats with extensive eel-grass (_Zostera_ spp.) beds bounded by a strip of cord-grass (_Spartina_ spp.) saltmarsh along the shore) from about 750 hectares of mainly sandflats (characterized by casts formed by lugworms (_Arenicola marina_) and a comparatively small _Zostera_ bed). This latter area, Holy Island Sands (abbreviated henceforth to HIS), included my main study sites.

III METHODS

1. General

Godwits were observed by means of a telescope (X20-X40) and binoculars (10 x 50). A X20 binocular microscope was used to examine gut contents of the birds. Substrate temperatures were measured at a depth of 3 cm before and after a period of observation.

Data were collected during the winters of 1970-71, 1971-72 and 1972-73.

2. Censusing

Godwits were counted twice monthly from October to the end of March. Counts were undertaken from about LW $1\frac{1}{2}$-3 ($1\frac{1}{2}$ to 3 hours after low water), as the birds were pushed by the flooding tide upshore of their LW feeding areas,but before there was appreciable movement between areas on the Lindisfarne Reserve. Birds were censused on HIS on one day and on the mud-and sandflats of the opposing mainland region on the following day; the two counts were taken as complementary. In the approximately fortnightly periods between counts, noticeable changes in numbers were noted.

The wardens of the Nature Conservancy Council counted all species of waders and wildfowl on the Reserve, usually once weekly, during autumn and winter. Their combined counts of godwits from roosts and feeding areas were 3 to 9 per cent higher than mine but included upwards of 130 birds which occurred on parts of the Reserve which I did not count, for example Budle Bay.

3. Measurement of diet

The composition of the diet of godwits on HIS was determined both through direct observation of feeding birds and by the analysis of the guts of birds shot whilst feeding.

The analysis of gut contents contains biases due to the different rates of digestion of small and large members of the same and different prey-species, and of hard-shelled and soft-bodied organisms. Furthermore, some species of waders get rid of indigestible material as pellets (Swennen 1971; Goss-Custard and Jones in prep.). These difficulties, reviewed by Goss-Custard (1973), were corroborated by my work with godwits in captivity. One bird, fed Nereis diversicolor for the last time in December and thereafter maintained on blowfly larvae, still contained two nereid jaws in its gizzard when shot the following June. This same bird was fed Arenicola marina, 3-5 cm in length, immediately before being shot. About 1 minute after it had swallowed the last Arenicola it was killed and within the following minute its gut opened and pickled. Of the 4 worms it had ingested in the 9 minutes available for feeding, only one was identifiable in the proventriculus. In view of these complications, more reliance has been placed on direct observation of feeding birds than on gut contents.

Worms over 3 cm in length can be seen without difficulty when they are taken by godwits. Lengths of worms in the diet were estimated by comparing them with the bill-length of the bird which took them. Four broad categories of worm-length were designated: 0-5, 6-10, 11-15 and 16-20 cm, respectively. The bill-lengths of male and female godwits (which are separable in the field) were taken arbitrarily as 8 and 10 cm, respectively, very close to the actual mean values (Behaviour, section V).

Worms, particularly Nereis, tend to stretch when extracted from the substrate. Longer ones are often broken into two or more pieces. An attempt was made to correct the worm-lengths observed to their unstretched lengths and to estimate total lengths for those which were extracted in several pieces. If only a short piece of Arenicola was extracted, it was assumed to be a tail, as virtually all Arenicola were taken from their tail-shafts. A tail frequently had one,or more,short thin strips of flesh hanging from it.

The larger bivalves taken were indentified easily as such. Bivalves less than 1 cm in length could not be recognized as such. However, if a bird manipulated a small prey item with relatively rigid opened mandibles, this indicated that a small bivalve rather than a small worm had been taken.

There was more difficulty in separating by direct observation small Arenicola and Nereis, less than 3 cm in length, from Scoloplos armiger, a small, narrow polychaete, not all of which were visible to me. With experience, separation was possible indirectly, using both the relative speed of handling and swallowing, and the degree to which the mandibles were open when the item was ingested. Furthermore, the behaviour of the bird could also provide an indication of the type of prey taken. For example, godwits often deviate from their direction of movement when responding to the cast formation of Arenicola. This prey is most vulnerable to predation when forming its cast.

The composition of the diet of godwits was determined by direct observation of feeding birds from dawn to dark on a total of 6 days in October, 5 in December and 4 in April as the birds moved with the tide over HIS during both spring and neap tides. The data obtained give a representative and seasonal picture of their diet on the study area. Additionally, the guts of twenty-four godwits shot while feeding actively on HIS were examined to obtain measures of the proportions of the various size-classes of bivalves taken and to look for identifiable remains of worms in the oesphagus and proventriculus.

4. Measurement of food intake during daylight hours

Observations of food intake were made on HIS. Birds were observed continually from dawn to dark on both spring and neap tides except when they were at HW roost. HW of spring and neap tides occurred in late afternoon and late morning, respectively. Spring tides completely covered the feeding areas of godwits; neap tides did not. Observations commenced at dawn or as soon as at least fifty godwits had returned from HW roost and started to feed. The birds were followed on foot as they moved with the ebb and flow of the tide. Most godwits flew S.S.E. from their HW roost on the Sand Ridge to the eastern end of HIS where they commenced feeding. Later they moved west to the area east of the Low and finally N.N.W. to the HW roost (Fig. 1). Observations terminated when most of the birds had started to roost or when darkness fell.

The same individual godwit could not be followed for an entire period as birds frequently left a flock while others joined it. Much of this movement occurred between areas on HIS itself, but flight between HIS and other regions of the Reserve was often noted for approximately 2 hours immediately after the birds had returned from their HW roosts and from about 3 hours before HW until all had left for their roosts.

Thirty-two individual godwits, feeding actively, were observed every hour, each for 1 minute. Observations alternated between males and females in each of two feeding locations: 'at' and 'beyond the tide-line' (for significance, see Behaviour section V). I noted the numbers of each size-class of each species or type of prey taken each minute.

Every 15-20 minutes, the proportions of godwits feeding actively (or loafing) were noted and averaged later to produce an average feeding time each day for an 'average' godwit. It is assumed that the average proportion of the day used for feeding by all godwits observed is equal to the proportion of the day that each individual feeds (Goss-Custard 1969; Heppleston 1971). This is valid only if feeding and non-feeding birds are equally visible, as was believed to be the case in godwits.

The data were collected on 3 days of spring and 3 of neap tides in October, 3 of spring and 2 of neaps in December and on 2 of springs and 2 of neaps in April. On all days, the substrate temperatures were above 3°C, the critical temperature below which some prey show reduced activity. Information from 1 day each of spring and of neaps with substrate temperature of +1°C was obtained in December. Additional data were collected for parts of days in all these months but are incomplete because of major sources of disturbance, particularly successive low flying aircraft, wildfowlers and unexpected changes in weather.

5. Studies of birds in captivity

Godwits were caught under licence from the Nature Conservancy Council and the primaries of one wing clipped. They were kept in a wire-mesh cage enclosing 5 m^2 of ground. A layer of straw bales was placed around the perimeter of the cage against the wire to prevent the birds injuring themselves by putting their bills through the mesh.

Birds were kept for 1 month before measurements of food intake were initiated as King and Farner (1959), working with White-crowned Sparrows (*Zonotrichia leucophrys*), found that weight changes, due mainly to muscular atrophy, were completed within this period.

The captive godwits were maintained chiefly on a diet of blowfly larvae (*Calliphora* spp.). These larvae were used exclusively during trials to estimate food intake during daylight hours. The captive birds used in these trials had larvae available at all times.

During trials, 800 larvae were presented in an enamel tray to the bird at dawn. Those remaining at dark were removed and counted. Several trials were attempted at night but mice were suspected of taking larvae on two occasions and dampness enabled some larvae to climb out of the tray on others. These data therefore are not included and only those data collected on days without disturbance to the birds are presented.

6. Calorific contents

Approximately equal numbers of the four size-classes of *Arenicola* were collected in September, December and May. A number of *Scoloplos*, and tails of *Arenicola* equivalent in length to animals of the first three size-classes of whole *Arenicola*, were obtained in September. The invertebrates were dried in a vacuum oven at 60°C. Calorific contents of the dried items were determined with a Gallenkamp ballistic bomb calorimeter, which is most accurate for heat releases of about 2 Kcals. No attempt was made to remove sediment ingested by the worms before they were burnt, since the period of starvation needed to clear their guts might have reduced their calorific content. Before each of the three periods of 'bombing', a calibration curve was obtained by combustion of 10 pellets of 5 different weights of dried AR benzoic acid. Because whole worms in each of the size-classes of Arenicola varied in length by up to 5 cm, dry weights and calorific contents were rather variable and no significant differences were apparent between results from the three sampling periods. The data for each size-class have therefore been pooled.

The energy contents of blowfly larvae, used in the studies of captive birds, were determined in the same way.

Basal metabolic rates of godwits were calculated using the formula for non-passerines of Lasiewski and Dawson (1967) based on lean body weights.

IV RESULTS

1. Godwit numbers

Monthly means for the three winters of study are tabulated below; differences amongst years were slight. Average numbers between October and March inclusive were:

October	2500
November	3500
December	4500
January	3500
February	2500
March	1500

The first major arrivals of godwits at Lindisfarne occur in August. These are chiefly juveniles. Adults do not usually return until they have completed moult of their flight feathers, some in September, but most in October (Chapman 1907; Evans & Smith 1975). Numbers remain relatively steady from November to February, though marked influxes have occurred briefly in some years, e.g. in December 1971 when numbers rose to 6000 for 2 days, and in January 1973 when they reached 5000 for 3 days.

Godwits comprise about 10 per cent of the total wader population wintering at Lindisfarne. The area ranked thirteenth in importance for waders amongst British and Irish estuaries in the winter of 1972-73 (Prater 1974), and held approximately 12 per cent of the Bar-tailed Godwits wintering in Britain.

2. Diet on Holy Island Sands

Godwits took two main prey on HIS, the polychaetes *Arenicola marina* and *Scoloplos armiger*. Table 1(a) summarizes the numerical composition of the diet in different months, based on observations during daylight hours. Table 1(b) indicates the relative contributions of the different sizes of prey to the total biomass intake. These figures are necessarily somewhat imprecise, because no attempt was made to clear sediment from the

Table 1a. The diet of Bar-tailed Godwits on Holy Island Sands during daylight hours at substrate temperatures above 3°C

Prey	Size-class	Per cent of total number of items taken in daylight					
		October		December		April	
		spring tides(3)*	neap tides(3)	springs(3)	neaps(2)	springs(2)	neaps(2)
Arenicola							
whole worms	I (0-5cm)	8½	8½	11	7	7	7
	II (6-10)	22	22½	19	22½	21½	20
	III (11-15)	6½	5	6	5	7½	6
	IV (16-20)	½	½	½	½	½	½
tails	I (0-5)	½	1	1	0	½	0
	II (6-10)	3½	2½	3	2	4	3
	III (11-15)	1	1	1	0	1	½
Scoloplos		57½	59	59	61½	57½	62½
Total number of worms taken		595	646	615	654	544	535

*Figures in parentheses are the number of days, dawn to dark, observed

Note: a) percentages are derived from the absolute values given in Table 3a

b) small numbers (less than 5 per cent of total items) of bivalves and other polychaetes were taken (see text for details)

Table 1b. The diet of Bar-tailed Godwits on Holy Island Sands during daylight hours at substrate temperatures above 3°C

Prey	Size-class	Average per cent by numbers*	Average dry weight (g)/size-class**	Average per cent by weight
Arenicola				
whole worms	I	8	0.05	4
	II	21	0.27	52
	III	6	0.50	27
	IV	½	0.86	4
tails	I	½	0.04	0.002
	II	3	0.13	3
	III	1	0.43	4
Scoloplos		60	0.01	6

*Figures are the averages of the values for the six date/tide periods given in Table 1a.

**These values include some sediment (see text) worm guts before they were dried and weighed. (It would have been necessary to keep the worms in clean seawater for several days to remove all sediment, and this would probably have reduced their calorific content, as mentioned earlier). Although Scoloplos contributed 60 per cent of the worm diet in terms of numbers taken, it provided only 6 per cent of the biomass intake. Hence Arenicola was by far the most important prey.

Several other invertebrate species were taken at times, but these never contributed more than five per cent of the total number of items seen to be eaten during daylight hours. Analyses of the contents of the oesophagus and proventriculus of twenty-four shot birds are given in Appendix I. These established the importance of Arenicola as the major annelid prey and confirmed that Scoloplos was taken, but suggested that cirratulids and oligochaetes may also feature in the diet at times. Oligochaetes are not common on Holy Island Sands, though cirratulids are in places. By direct observation, it is not possible to distinguish Scoloplos and cirratulids taken by godwits, so some of the latter may have been included under the Scoloplos heading in Tables 1(a) and (b). Since their biomass is even smaller than that of Scoloplos, the predominant importance of Arenicola in the godwit diet remains unaltered. On spring tides only, beds of the tube-building polychaete Lanice conchilega became available to godwits at the lowest tidal levels, and a few of these worms were taken. Another polychaete, Nereis diversicolor, was also taken occasionally, but it was not common on Holy Island Sands, as it prefers substrates with brackish rather than fully saline interstitial water.

Bivalves formed the other group of invertebrates taken regularly, but in small numbers. Since different species could not be distinguished by direct observation, all bivalves have been treated as if they were Macoma balthica for later calculations of calorific intake. Gut analyses (Appendix I) of godwits shot at all tidal levels confirm that Macoma, or the very similar Abra tenuis, were the species most often taken, as was to be expected in view of the more restricted distributions and lower densities of *Cardium* (= *Cerastoderma*) *edule*, *Scrobicularia plana* and *Tellina tenuis* on the study area. Measurements of the *Macoma* found in the shot birds have been used to calculate the proportions of different size-classes taken, since these could not be observed directly.

Numbers of bivalves, *Nereis*, *Lanice* and other items seen to be taken during day-long observations of godwit feeding are summarized in Table 3(b).

3. Energy intake

The calorific contents of the foods taken by godwits during daylight hours at different times of year are summarized in Table 4. Tables 2 and 3(a) and (b) show the derivation of the figures presented in Table 4.

Although the energy intakes during daylight hours at temperatures above 3°C appear to vary little with season or tidal range, those for December are probably the most accurate values of the intake of a single godwit. In December, all birds fed for most of the time when their feeding areas were uncovered by the tide during daylight hours. In autumn and spring, the average duration of feeding by an individual godwit may have been overestimated, since measurements of the proportions of birds feeding and not feeding were made on flocks whose individual composition changed during the period of observation. If satiated birds had tended to leave the flock, and hungry birds to join (after feeding elsewhere on the Lindisfarne Reserve), overestimation would have resulted.

In December, the total calorific intake of godwits decreased drastically on cold days, even though they fed for longer than on warm days. Spring tide conditions were less favourable than neap tides, since the number of hours for which the feeding grounds were uncovered during daylight were reduced from 6.8 to 5.8. As shown in Table 4, birds fed throughout the time available on both days. In spite of this, they failed

Table 2. Calorific contents of Arenicola marina, Scoloplos armiger and blowfly larvae

Prey & size-class	Total No. of each size-class used	No. of pellets made & bombed	Average calorific content/worm (Kcal)
Arenicola - whole worms			
Size-class I	63	11	0.12
II	52	28	0.65
III	41	41	1.48
IV	23	29	1.80
Arenicola - tails			
Size-class I	23	3	0.08
II	18	6	0.28
III	4	4	0.55
Scoloplos	110	3	0.03
Blowfly larvae	150	6	0.12

Table 3a. Food intake (species and numbers of each size-class) of Bar-tailed Godwits in autumn, winter and spring during daylight hours at different substrate temperatures

Month	Tide	Substrate temp. (^{o}C)	*Arenicola* size-classes							*Scoloplos*
			I (0-5cm)		II (6-10)		III (11-15)		IV (16-20)	
			worms	tails	worms	tails	worms	tails	worms	
October	springs(3)[*]	> 3	50	4	132	21	39	5	3	341
	neaps(3)	> 3	56	7	144	17	33	8	2	379
December	springs(3)	> 3	68	5	117	18	36	6	2	363
	neaps(2)	> 3	46	1	144	13	31	7	3	389
	springs(1)	+ 1	37	2	60	6	19	3	3	341
	neaps(1)	+ 1	30	1	102	7	18	4	4	263
April	springs(2)	> 3	39	2	118	23	42	5	3	312
	neaps(2)	> 3	37	1	106	16	33	4	3	335
Average dry weight(g)/ item[**]			0.05	0.04	0.27	0.13	0.50	0.43	0.86	0.01
Average calorific content/item (Kcals)			0.12	0.08	0.65	0.28	1.48	0.55	1.80	0.03

[*] Figures in parentheses are the number of days, dawn to dark, observed

[**] These values include some sediment (see text)

Table 3b. Food intake (species and numbers of each size-class) of Bar-tailed Godwits in autumn, winter and spring during daylight hours at different substrate temperatures

Month	Tide	Substrate temp. (^{o}C)	Bivalve size-classes			*Nereis* size-classes		*Lanice* size-class
			I	II	III	I	II	I
			(<6mm)	(7-12)	(13-15)	(0-5cm)	(6-10)	(5-10cm)
October	springs(3)[*]	> 3	3	6	7	3	6	19
	neaps(3)	> 3	4	8	11	4	8	none
December	springs(3)	> 3	2	5	5	2	5	14
	neaps(2)	> 3	4	8	9	2	5	none
	springs(1)	+ 1	4	7	8	4	7	5
	neaps(1)	+ 1	3	7	7	2	3	none
April	springs(2)	> 3	1	4	4	3	6	6
	neaps(2)	> 3	3	4	5	2	3	none
Average dry weight(g)/item			0.003[+]	0.007[+]	0.028[+]	0.023[++]	0.085[++]	0.27[‡]
Average calorific content/item (Kcals)			0.02[+++]	0.04[+++]	0.14[+++]	0.11[++++]	0.40[++++]	0.65[‡]

[*] Figures in parentheses are the number of days, dawn to dark, observed

[+] From Prater (1972); [++] from Goss-Custard (1966); [+++] from Ingvarsson (1972);

[++++] from Joffe (unpub.)

[‡] Dry weight and calorific content of *Lanice* are taken as equivalent to a similar length of *Arenicola*

Table 4. Calorific intake of Bar-tailed Godwits in autumn, winter and spring at different substrate temperatures during daylight hours on spring and neap tides

Month	Tide	Substrate temp. (°C)	Average no. of daylight hours feeding/godwit	Average total intake (Kcals)/godwit	Calorific intake (Kcals)/ hour/godwit	Factor X BMR**
October (3)*	Spring	> 3	5.5	189	34.4	5.6
(3)	Neap	> 3	5.6	178	31.8	5.2
December (3)	Spring	> 3	5.0	170	34.0	5.0
(1)		+ 1	5.8	100	17.2	2.9
(2)	Neap	> 3	6.1	174	28.5	5.1
(1)		+ 1	6.8	118	17.4	3.5
April (2)	Spring	> 3	6.5	174	26.8	5.1
(2)	Neap	> 3	5.7	146	25.6	4.3

*Figures in parentheses are the number of days, dawn to dark, observed

**The Basal Metabolic Rate of an "average" godwit of lean weight 295g is 34.1 Kcal (see text) to obtain more than about two-thirds of their normal intake by day.

At temperatures above 3°C, godwits ingested food equivalent to just over 5 times their basal energy requirements. It is not known what proportion they assimilated, though it was presumably high, as faecal output appeared small.

4. Night feeding

On one to three dark nights each month from early October to the end of March during three years, I walked both along the tide-line of HIS and also parallel to it approximately 200 metres upshore. This was undertaken between $1\frac{1}{2}$ and 3 hours before and after LW on both spring and neap tides. On different nights, the same procedure was repeated along the tide-line between 3 and 4 hours before and after HW, on 11 occasions in December and January. As the substrate of the mudflats adjacent to the mainland is very soft, I walked along this tide-line only twice. The presence of godwits was noted by listening for alarm calls when birds were flushed, although only very qualitative information could be obtained of the numbers present. A shaded torch was used to examine the substrate for indications of probing.

During the periods of full moon the same procedure was followed on at least one night each month. By facing the moon, godwits could be seen quite easily although any items taken could not be observed.

(a) Dark nights

Few godwits were flushed from the tide-line on dark nights in October, early November, February and March, although no indication of birds present on the Sand Ridge, the chief daylight HW roosting area, was noted on two visits in October at the time of LW. A considerably higher estimated proportion of the total numbers present in December and January were thought to be along the tide-line in these months. At least some were feeding as indicated by probe-holes in the substrate. No godwits were flushed from upshore of the tide-line.

Godwits appeared to leave for, and return from, the HW roosting areas about an hour earlier and later, respectively, than would be expected on similar tides during daylight. However, on the only two cold nights (substrate temperatures of about 0 and +1°C) when I was on the flats, some birds were present along the tide-line until the feeding areas were covered and returned to them as soon as they were uncovered. At HW, the birds tended to roost at the tide-line in scattered groups. More call-notes were heard at night than during daylight.

For part of December and January in the winter of 1974-75 I had the use of an image intensifier, a night-viewing apparatus, whilst engaged in research on ducks, geese and swans at Lindisfarne. Incidental to this work, I obtained 103 minutes of observation on individual godwits during dark nights on HIS. These birds were all feeding along the tide-line; none were seen upshore. Although no measurements of the number of probes per minute were obtained, the birds appeared to be probing at a faster rate than during daylight. In this area, where, during the time of my studies on godwits, they would be expected to take appreciable numbers of <u>Arenicola</u> in daylight, at least no large <u>Arenicola</u> were taken. Only one large worm was captured, probably a <u>Nereis</u>. (Large <u>Nereis</u> tend to move more vigorously than <u>Arenicola</u> when first extracted from the substrate.) The distances at which the birds were observed with the image intensifier were too great to enable swallows to be seen. Presumably, the godwits were taking small items. Birds returned to the feeding areas after HW about an hour later than would be expected during daylight and some godwits were seen feeding along the tide-line on the mudflats adjacent to the mainland, again with the aid of the image-intensifier.

(b) Moon-light nights

Observations during periods of full moon on HIS support those made on dark nights. A higher estimated proportion of the total number of godwits present in mid-winter were feeding along the tide-line than in

Table 5. Calorific intake of Bar-tailed Godwits in captivity

Captive	Average Air temp. (^{o}C)	No. of days*	Average no. of Blowfly larvae taken/day	Average Kcals ingested/day	Average Kcals ingested/hour of daylight	Factor X BMR**
Juvenile male	warm (6-15)	6	677	80.6	9.2	3.1
	cold (-1 &+2)	2	705	83.9	10.5	3.2
Juvenile female	warm (11 & 14)	2	691	82.2	8.7	2.9
	cold (+2)	1	701	83.4	8.8	2.9

*Each day comprises the period dawn to dark

**BMR of male godwit (lean weight 237g) calculated as 26.0 Kcal/day;
that of the female (lean weight 273g) calculated as 28.5 Kcal/day

autumn and late winter. In mid-winter, the numbers present on the tide-line were highly variable, probably due to wildfowlers who were on the flats in considerable numbers on moon-light nights.

5. Daily energy intake of captives

The calorific contents of food eaten by two captive godwits are summarized in Table 5. Food was available only during daylight hours, at a calorific content per item of 0.12 Kcals (Table 2). Both captive birds had slightly greater energy intakes on cold than warm days.

The lean weights of the captive male and female godwits, 237 and 273 g, respectively, were less than the mean lean weights of male (270 g) and female (319 g) birds collected throughout the winter at Lindisfarne (Evans and Smith 1975). Consequently the calculated values of their Basal Metabolic Rates are lower than the figure of 34.1 Kcals/day used in the calculations in the previous section. (This figure was appropriate to an "average godwit" of weight 295 g, since observations on feeding rates and food consumption were made on approximately equal numbers of males and females).)

6. Effects of wind and rain upon feeding

During gales, most godwits fed for 22 to 38 minutes longer (14 periods of observation) than on calm days with similar spring and neap tides. Most birds were found feeding on lee shores and along the edges of sheltered channels. Between 24 and 69 per cent of the total number of birds counted on each day of gales were feeding upshore of the tide-line, on wet areas of substrate, whereas on calm days 84 to 90 per cent fed along the tide-line. Distances between individual feeding godwits appeared smaller than on calm days but no quantitative data on feeding behaviour were obtained, chiefly because it was impossible to hold telescope or binoculars sufficiently still.

During severe gales, godwits were seen to spend a high proportion of their time loafing at HW roosts and on lee shores, and some apparently fed only around the time of mid-tide. Sustained periods of observation could not be undertaken, so these impressions cannot be quantified.

On days of light rain no differences were noted in the behaviour and feeding locations of the birds from the situation on dry days. During heavy rain, however, a higher proportion fed upshore of the tide-line and, as during gales, the birds seemed closer together. Quantitative data were not collected.

V DISCUSSION

(1) The diet and time required for feeding

On Holy Island Sands at Lindisfarne, Bar-tailed Godwits take chiefly *Arenicola marina* and *Scoloplos armiger*, the former predominating in biomass and energy content, the latter in numbers taken. This raises the question whether godwits are selecting these two from amongst many potential prey-species, or whether they are taking the most abundant prey within their chosen feeding habitat. In other areas, limited information has been collected recently on the diet of godwits. This is tabulated below.

Feeding locality	Chief prey	Authority
Morecambe Bay, Lancashire	bivalves, nereids, *Arenicola*	Prater (1970)
Dee estuary (central part), Cheshire	*Macoma balthica*	N. E. Buxton (pers. comm.)
Teesmouth, Cleveland	*Nereis diversicolor*, some *Arenicola*	Evans (pers. comm.)
Waddenzee, Netherlands	annelids, *Macoma*	Rooth (1960) Boer & Monsees (1967)
The Wash (eastern side), Norfolk	*Macoma*, *Lanice conchilega*	J. D. Goss-Custard (pers. comm.)

These data suggest that godwits will take a variety of prey, chiefly large polychaetes and bivalves, and that not all prey-species that might be taken are in fact exploited in a given locality. For example, although *Macoma* is taken commonly in several places, it is rarely utilized at Lindisfarne. From information on invertebrate densities in the different localities, it appears that godwit diets are not determined by the absolute densities of prey available, but rather by the relative abundance of different prey. Morecambe Bay supports appreciable densities of *Arenicola* (from 20-100/m^2; Anderson (1972)), comparable with those found in my study area at Lindisfarne (25-30/m^2), yet *Arenicola* was not of such overriding importance in the diet of godwits there (Prater 1970). However, densities of *Macoma* were much higher on Morecambe Bay than at Lindisfarne, reaching 2000-4000/m^2 in the highest density zones, by comparison with a maximum of about 500/m^2

on Holy Island Sands (W.F. Miller & A. Turk, Unpublished). Macoma was also much more widely distributed at Morecambe than at Lindisfarne. Hence the occurrence of a higher proportion of Macoma in the diet of Morecambe Bay godwits is explicable if they take the commonest suitable prey.

The plasticity of diet of godwits emphasizes the need to provide information on prey availability when descriptions of avian diets are published. It is most unlikely that long-distance migrants such as godwits would select prey of specific identity at various points along their migration routes. More probably, the identity of the prey taken is determined by the type of cues to which the godwits respond while foraging. Indeed, if godwits sought particular prey, they would be restricted in terms of potential wintering areas to those estuaries where those prey were available. This would mean that godwits specializing on Arenicola would be unable to use muddy estuaries where this prey was absent, even though various nereids were present. Specialization in feeding has, of course, been recorded in Oystercatchers (Haematopus ostralegus) (Norton-Griffiths 1967), but these are short-distance migrants, and unusual amongst waders in that they feed their young, which allows the maintenance of specialized feeding habits from generation to generation.

In places where a range of potential prey-species is available, the diet of a predator may change seasonally, according to changes in absolute, and therefore relative, abundance of possible prey. Such changes may be considerable. Anderson (1972) noted a 50 per cent reduction in the densities of Macoma on Morecambe Bay between autumn and the following spring, and Goss-Custard et. al. (1974) demonstrated by use of an exclosure a 43 per cent decline in numbers of the sedentary polychaete Lanice during the course of a winter. These declines may have been attributable to predation by waders, though Anderson believed a poor spat-fall of Macoma to have been responsible. At Lindisfarne, godwits may remove 26 per cent of the standing crop of Arenicola during the winter (see Appendix II).

While different species of prey may provide adequate diets for godwits, some prey may be considerably better than others if they provide a higher calorific return for each item obtained. If prey availability is comparable, one would expect godwits to have to feed for a shorter time each day to satisfy their energy requirements on a diet of large Arenicola than on the smaller Nereis. Data from Seal Sands, Teesmouth (P. J. Knights, pers. comm.) enable such a comparison to be made. The data are tabulated below.

Date	Locality	Prey	Hours of feeding during daylight	Worms taken/ min
October	Lindisfarne	Arenicola	5.5 (spring tides) 5.6 (neap tides)	1.2
October 1973	Seal Sands	Nereis	7.0	1.4
November 1973	" "	"	7.7	1.2
October 1974	" "	"	5.8	1.8
November 1974	" "	"	7.0	1.4

As may be seen, when prey availability allowed the same rate of capture of worms at the two localities, godwits had to feed for about 2 hours longer on a diet of Nereis than on Arenicola. However, changes in prey availability also affect the rate, and therefore the duration, of feeding, as the Teesmouth figures show. Nereis densities were higher in the autumn of 1974 than in autumn 1973 (Evans, pers. comm.).

The question arises whether the godwits were feeding as fast as they coul when prey availability was not limiting the rate of food intake, that is, at temperatures above 3°C for Arenicola in my study area. Food intake should be greater in mid-winter than at warmer temperatures in autumn, yet the hourly rates of energy intake in October and December at Lindisfarne were very similar (Table 4), even though the hours of daylight available for feeding were longer in October than December. Thus, godwits would seem to be feeding as fast as they can so as to minimize the time spent feeding. Heppleston (1971) claimed that Oystercatchers took less mussels (Mytilus edulis) per hour in December than in October, for reasons unknown, but as his January observations revealed a feeding rate identical with that in

October, it is difficult to reject the idea that birds were feeding as fast as they could in all months.

(2) Seasonal changes in energy intake in the non-breeding season

The results in Table 4 show that there were slight seasonal differences in daily energy intake which may be attributable to several factors.

a) During moult, metabolic rates, and often also body temperatures, are raised to counteract surface heat losses when insulation provided by plumage is less (Payne 1972).

b) Resting energy requirements must be higher in colder weather, unless the thermoneutral zone is very wide, with a lower critical temperature near freezing point.

c) Energy intake must be higher than normal daily requirements if fat is to be stored for migration or as a mid-winter reserve. Migratory fat is normally laid down very quickly; the mid-winter reserves are gained more slowly (King 1972). One would therefore expect a marked increase in daily energy intake chiefly before migration.

When considering the Lindisfarne results in terms of the above, it should be noted that the values for daily calorific intakes refer to the hours of daylight only, and that the intakes in October and April are possibly slight overestimates, as discussed previously. In addition, the values apply to an "average" godwit, a compromise between adults and juveniles, males and females.

i) October. In this month, most juveniles have finished moulting but those adults which have just arrived, or which arrived in August in breeding plumage, are still completing the moult (Evans & Smith 1975). Therefore, the value of daily energy intake for the "average" godwit should be slightly higher than "existence energy". Although estimates for non-passerines are not available, in most moulting passerines so far studied, the metabolic rate increased from 5 to 30 per cent above the rate of non-moulting birds (Payne 1972). Apart from this complication, the value obtained should be close to the true daily energy requirement appropriate to October temperatures, since almost all food was obtained by day.

ii) December. Godwits fed at night in December much more than in autumn or spring, although the proportion of the population engaged in night-feeding could not be determined. It appeared that they were not obtaining Arenicola at night, so must have been ingesting smaller prey-items, which would have produced a lower hourly calorific intake.

Allowing for the additional food ingested at night, godwits will have taken substantially more than the daytime intake of 170 Kcals during each 24 hours in December when temperatures were relatively warm. Under these conditions they could maintain weight and possibly store a little fat in spite of lower night temperatures than in October.

During cold days in December, however, the intake of godwits was reduced to $^2/_3$ of that on warmer days (because of reduced availability of prey; see Behaviour paper). Yet the total energy required should have been greater than that obtained during the warmer days. Thus, intake at night must have been of crucial importance. An indication of its extent is provided by calculations based on changes in body composition. During a period of 5 cold days in December, 1970, the lipid index of adults and juveniles fell by 1.3 and 4.0 per cent, equivalent to losses of 5 and 20 g of fat, respectively (Evans and Smith 1975). This indicates that adults and juveniles must have used up about 9 and 36 Kcal of fat per day, respectively. Since their daytime food intake was about 110 Kcal on cold December days, by comparison with 170 during warm weather in December, they must have been able to obtain during the cold weather minima of about 50 Kcal (adults) and 25 Kcal (juveniles) at night, over and above the normal night intake in warmer weather. (These calculations assume that the two age-groups are equally efficient by day.) The figures suggest that adults may be able to obtain almost as much energy by night as by day during cold days, yet without taking Arenicola. If they are so competent at feeding by night on other prey, why do they not take these by day? The probable explanation is that godwits detect the presence of Arenicola visually (by cast formation) but this is not possible at night, when prey-items must be detected chiefly by tactile means. Possibly certain prey such as Nereis may also change their behaviour to become more available by night (Vader 1964). Low temperatures might provide a higher proportion of lamellibranchs in shorebird diets, as Prater (1970) reported that the shells gape as the adductor muscles relax with torpidity, and are then frequently washed to the surface, where they would be more vulnerable to predation.

During very cold weather, the feeding situation becomes critical for waders. Data from one very cold day (substrate temperature -4°C; Table 15, Behaviour paper) can be used to calculate that godwits could not have obtainec more than approximately 15 Kcal during daylight hours, by feeding mainly on Scoloplos (since no Arenicola are available at such low temperatures); presumably, they obtained even less by night. Two questions are raised: do godwits "sit out" cold spells, or if they emigrate, how soon do they leave? In mid-winter about 12 per cent of their total body weight is fat (Evans and Smith 1975), so they could survive for about three days without food. Clearly, they stayed and lost fat when temperatures fell to around 0°C (see earlier), but in really hard times, many may move. Pilcher (1964) reported that during the hard winter of 1962-63 on The Wash, where the cold spell commenced on 26 December, godwit numbers had decreased noticeably early in January and that few were left by the end of the month; compared with other wader species, few were found dead. However, Chapman (1907) wrote of godwits at Lindisfarne that "it is in fact during the hardest weather and most protracted frosts of mid-winter that godwits become most numerous". He may have meant "concentrated", as I have noted that on very cold days the birds are restricted to feeding at the tide-line in those few areas free of slush and ice, where indeed they seem numerous.

If the weather becomes very cold, it would be of survival value to move, even if temperatures rise again rapidly, since permanent damage may be done for at least that winter to invertebrate populations. For instance, the ice-winters of the early 1940's severely reduced the populations of Arenicola and the bivalve Scrobicularia plana on the Wadden area east of the Skalling peninsula (Smidt 1944). Indeed, Scrobicularia populations in Morecambe Bay were apparently still recovering in 1969 from the effects of the severe winter of 1962-63 (Anderson, 1972). Additionally, cold may stimulate downshore migration of some invertebrates. Goss-Custard (1974) has evidence for movements in Macoma and Vader (1964; quoting Verwey 1958) noted that there were indications that Nereis and Arenicola attempted to migrate downshore in very cold spells. If such movements of invertebrates are extensive during cold weather, but the animals return upshore as soon as temperatures rise, then godwits might survive better by staying than by moving during short cold spells; but no information is available on any return movements of the invertebrates.

iii) April. During this month the godwits studied could have been preparing for migration. Evidence reviewed elsewhere suggests that those present in Northumberland in April are chiefly passage godwits (Evans 1966) or those which oversummer at Lindisfarne, as most of the overwintering birds depart by late March. The passage birds may not fly far when they leave Lindisfarne, as godwits collected in April had relatively low fat levels (Evans & Smith 1975). Therefore, the energy intake I measured in April is probably not much above the existence energy, particularly since little night feeding was recorded. One would have expected to find a higher daily food intake just prior to the departure of overwintering godwits,as it is well documented for many passerines (e.g. King 1972) and also for some waders (Pearson et al. 1970; Minton 1973) that their weights rise rapidly before migration. Such weight increases are attributable chiefly to storage of fat to serve as fuel for the flight.

To summarize, during October and April godwits must have ingested enough energy to meet their daily requirements, and perhaps slightly more, during daylight hours. To do the same on warmer days in December, some night feeding was required, but this may have become extensive during cold weather in that month.

(3) The relation of food intake to basal metabolic rate

For its predictive value, it is useful to know whether different species taking similar types of prey require a normal daily energy intake which is an approximately constant multiple of their basal metabolic rate at a given time of year. Any such factor is unlikely to be highly constant because of (i) differences between species in feeding methods, which could lead to different amounts of energy being spent in feeding, and (ii) differences in the efficiency of assimilation of similar prey. The latter effect is likely to be only slight.

The October and April values for daily energy intake of godwits indicate a multiple of approximately 5 X BMR for energy obtained during daylight hours. Values in the literature for daily food intake of other species of waders include varying sources and degrees of errors, chiefly because they were by-products of studies designed with other aims, and were obtained at different times of year. Using the data of Davidson (1968) and calorific values for cockles (Cardium edule) provided by Hulscher (1974), the daily calorific intake of Oystercatchers may be calculated as 6.8 times the BMR. Data from Prater (1972) indicate that Knot (Calidris canutus), feeding mainly on Macoma, ingest a maximum of 6.7 X BMR,assuming that their food intake at night equals that by day. Prater thought that Knot acquired only 25 per cent as much energy by night as by day but this is probably an underestimate because Knot feed chiefly by non-visual means. (Prater's figure would give a factor X BMR of 3.8.) The multiple X BMR for Redshank (Tringa totanus) feeding on the amphipod (Corophium volutator) and Nereis was calculated by Goss-Custard (pers. comm.) as 4.6 to 4.8.

Thus, waders may require 4 to 6 X BMR to satisfy their daily energy requirements at different times of year.

It is of interest to compare an herbivorous species with waders. White-fronted Geese (Anser albifrons), feeding upon grass, ingested 5.0 times their basal energy requirements (Owen 1972). However, the energy assimilated undoubtedly differs between herbivorous and carnivorous birds. Ebbinge et al. (1975) found assimilation efficiencies of only 33.2 and 21.7 per cent for captive and free-living Barnacle Geese (Branta leucopsis), respectively, feeding on various grasses. At the other end of the trophic pyramid, captive Great-horned Owls (Bubo virginianus) assimilated 85 per cent of their mouse diet (Duke et al. 1973).

My captive godwits, feeding on maggots, ingested about 3 X BMR, all during daylight hours, about $^3/_5$ of that of free-living birds. Oystercatchers in captivity had an intake of 4.3 X BMR (Hulscher 1974), but they were fed on mussels which, as in the wild, they had to open before they could obtain the flesh. Hence, it is not surprising that they had to expend more energy, in relation to BMR, and therefore body size, than the godwits in captivity.

The results from captive godwits indicate that if no appreciable energy is used for food gathering and flying to and from roosts, then an energy intake of only 3 X BMR is required. Thus, the cost of food gathering appears to be about 2 X BMR, almost as much as that of keeping alive.

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The Feeding Behaviour of the Bar-tailed Godwit

I INTRODUCTION

To survive a winter's day, an avian or mammalian predator must obtain, on average, enough energy from its food to balance that needed to maintain its body temperature and expended to capture its prey. In simple predator-prey situations, the prey are always available to the predator if only the latter can detect them; the prey escape detection by crypsis, or by immobility if disturbed. In a more complex situation, such as the one to be considered in this paper, the prey are available to the predator only occasionally, and even then can escape capture by moving out of reach if disturbed. The study reported here was aimed to find out how the behaviour of a large shorebird, the Bar-tailed Godwit Limosa lapponica, was adapted to enable it to exploit effectively its main prey, the polychaete worms Arenicola marina, Scoloplos armiger and Nereis diversicolor. Most attention was paid to the interactions between godwits and Arenicola, since this prey was less readily available to the birds than the other two species, yet formed the most important component of the diet in energetic terms.

As will be shown, the availability of Arenicola is influenced by a wide variety of inter-related factors, among the most important being the temperature and wetness of the sandy substrate in which the worms live. Changes in the behaviour of Arenicola are accompanied by changes in the feeding behaviour of the godwits, particularly in terms of the size of the area searched by an individual in unit time, and its proximity to other feeding godwits. As godwits normally feed in flocks, information was also collected relevant to the different hypotheses of the survival value of flocking (cf. Murton 1971a; Lazarus 1972), and it will be shown that birds in flocks both feed more successfully and stand less chance of being taken by birds of prey than birds feeding singly.

Although the major aim of the study was to investigate adaptations of the behaviour of a predator to the behaviour of its prey, the predator chosen was sexually dimorphic, with females larger than males, as in most wading birds and more especially in birds of prey. This necessitated separate study of the feeding behaviour of male and female godwits to find out whether, and if so how, dimorphism reduced competition between the sexes at those times of year when survival was most difficult. Various hypotheses of the advantages of sexual dimorphism have been considered by Reynolds (1972), particularly as they apply to birds of prey, and they are discussed further here in the light of my observations of the behaviour of godwits, especially in very cold weather when prey availability was reduced severely.

II STUDY AREA

Two study sites were located on the Lindisfarne National Nature Reserve (see Ecology section II for general description) in north Northumberland, one on Holy Island Sands (HIS) and the other at Sandon Bay (SB).

The study area on HIS comprised a strip of sandflats 400 and 200 m wide at the top and bottom, respectively, extending downshore from just below the high water mark for 950 m to the edge of a major channel (Fig. 1). A smaller drainage channel ran for about 580 m of its length. The substrate consisted of wet and dry areas of sand. Dry areas were slightly higher in elevation. The invertebrate fauna consisted mainly of the polychaetes *Scoloplos armiger* and *Arenicola marina*, one cirratulid species, oligochaetes and the bivalve *Macoma balthica*. The substrate was relatively stable during the three winters of study (1970-71, 1971-72, 1972-73) although *Zostera noltii* began to encroach onto part of the western side of the area between the second and third winters; also, during the autumn of 1972, two small shellbanks formed.

Sandon Bay, directly exposed to the North Sea (Fig. 1), consists of a stretch of about 500 m of sandy beach bisected in the middle by a bar of basaltic rock. Both the topography and the densities of the invertebrate fauna, comprised mainly of oligochaetes and the polychaetes *Nereis diversicolor* and *Arenicola marina*, changed frequently during autumn and winter onshore gales.

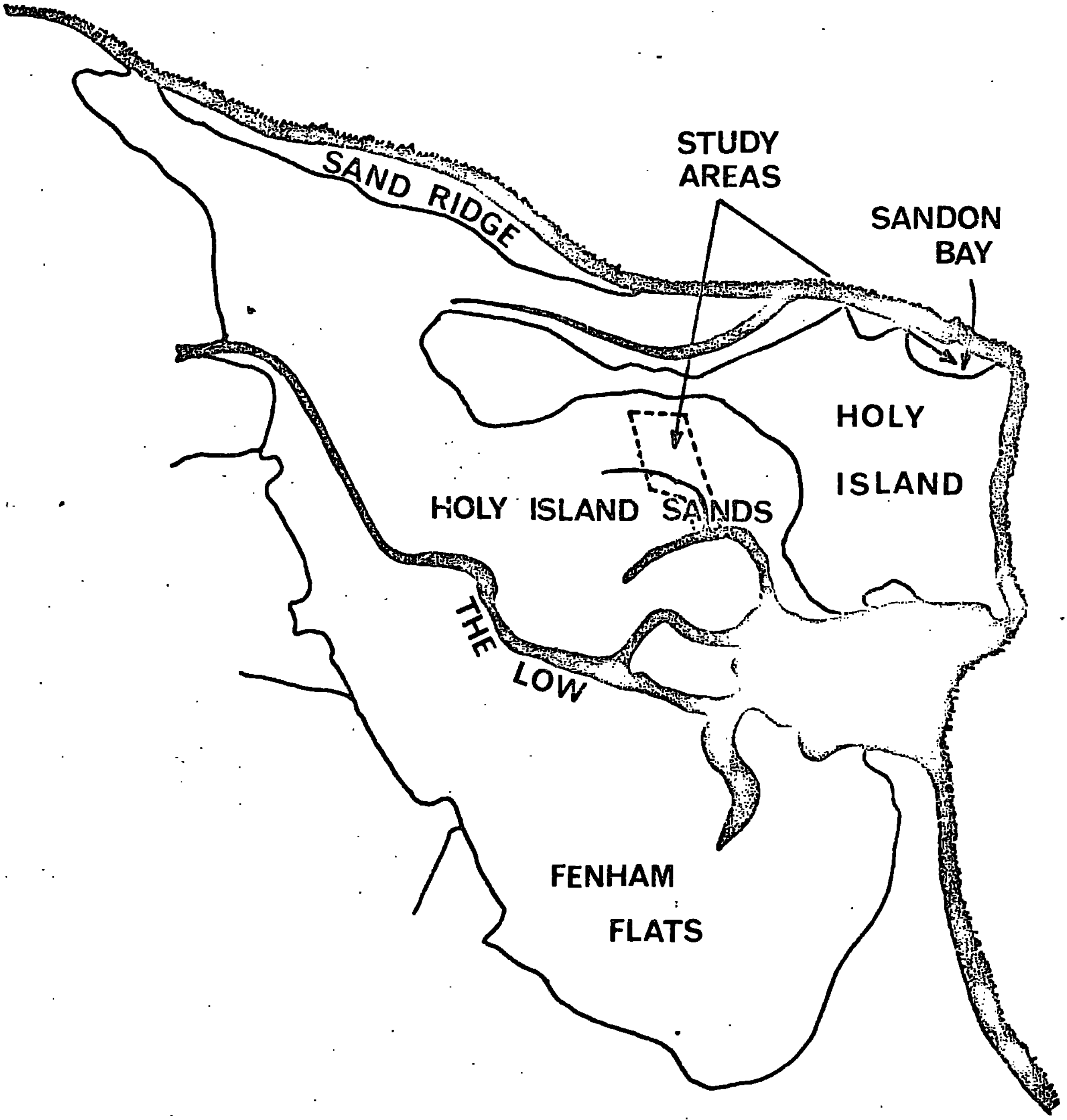

Fig. 1 The study area at Lindisfarne, Northumberland

III DESCRIPTION OF FEEDING BEHAVIOUR

Bar-tailed Godwits usually feed in flocks whilst walking briskly back and forth parallel and close to the tide-line. Often they feed in water to a depth where even their backs are covered; however, some feed upshore of the tide-line, on wet rather than dry areas of substrate. Birds walk quickly over dry substrates, probing less frequently than on wet areas. They detect their prey by both visual and tactile methods, but chiefly the former. Usually, a godwit inserts its bill shallowly into the substrate in a series of trial probes, but upon detection of a prey-item the bill is inserted to full length. Several deep probes are often required to extract a large prey-item; during these, the bird pivots around the hole. Smaller prey-items are swallowed while the bill is still inserted in the substrate (godwit throat movements are observed easily). Large worms are often washed before being swallowed. Stitching, a series of very rapid shallow probes, is infrequently used. Swishing, i.e. lateral movements of the bill through the substrate, was not seen at Lindisfarne, where most godwits feed on sandy substrates.

IV GENERAL METHODS

On HIS, observations were made chiefly from hides, left in place from early autumn to late spring, constructed from straw bales wrapped in chicken wire and staked to the substrate. Observations were also made on HIS by approaching the birds on foot as closely as possible. At SB, observations were made from the sand dunes parallel to the beach. A telescope (X20-X40) and binoculars (10 X 50) were used to observe the birds from ranges between 30 and 200 m. Observations were timed by stop watches. Data were recorded on tape and transcribed later. It was difficult to acquire detailed data from individuals in flocks of more than 30, so, in general, observations of larger flocks were not made. Unless otherwise noted, the numbers of males and females in a flock under observation were approximately equal and data on birds-of-the-year are excluded. Substrate temperatures at a depth of 3 cm were taken to the nearest 0.5°C before and after a period of observation which extended for between 40 and 100 minutes.

Appendix II should be referred to for details of invertebrate sampling.

Terms used in description of feeding behaviour, and the sequence of observations.

a) Probes and items taken per minute. Self-explanatory. All probes directed at one item were included.

b) Nearest neighbour. Nearest neighbour is the distance between the observed bird and its nearest neighbour and was determined by using bird-length as a measure. (One bird-length, head to tail, equals 25 cm; male and female are of about equal length, excluding bill-length). Observations on nearest neighbour were made immediately before and after each minute of observation of probing and items taken, and after each minute of observation of the area searched. These three observations were made for each bird in each sequence of observations.

c) Area searched. The area searched is defined as the minimum area traversed by a bird in unit time. This area and its shape were determined by observing the bird for one minute and recording the number of bird-lengths the godwit travelled in its main direction of movement and the number of deviations made from the latter. The angle of each deviation from the birds' main direction of movement was estimated to the nearest 10 degrees. Subsequently, these data were plotted on graph paper with a protractor to determine the area searched and its outline shape.

d) Flock location and flock shape. The location of the flock and its outline shape were noted in relation to the tide-line. The length of the flock was determined with reference to series of stakes placed at 25 m intervals along a succession of positions of the tide-edge. The breadth of the flock was estimated by eye in relation to the tide-line and the point at which the birds were 'knee-deep' in water. The proportion of birds 'at the tide-line' and 'beyond the tide-line' was noted. Birds upshore of the tide-line or wading in not more than 'knee-depth' of water are described as 'at the tide-line' and those wading over knee-depth as 'beyond the tide-line'. These data, together with nearest-neighbour distances and outline sketches of the flock enabled a description to be made of the flock: its location, shape and the distribution of birds within it. This information was collected before and after each period of observation of feeding behaviour.

e) Agonistic behaviour. Intra- and interspecific interactions between birds were noted for one or two minutes before and after each period of feeding behaviour. All the birds in the flock (or as many as possible) were observed simultaneously. The number of each of three categories of encounter, as well as the overall number of birds under observation, were recorded. The probability of encounter was calculated by expressing the number of encounters (including the number of birds involved in each encounter) as a proportion of the number of bird minutes observed.

In summary, the overall sequence of each observational period was: 1) flock location and flock shape; 2) agonistic behaviour; 3) feeding behaviour including the number of probes and items taken per minute, search area, and its shape, and nearest-neighbour distances of individual birds; 4) agonistic behaviour; 5) flock location and flock shape.

The specific sequence of feeding behaviour of individual birds observed was: 1) one observation of nearest-neighbour distance; 2) one minute of observation of probes and items taken; 3) one observation of nearest neighbour distance; 4) one minute on search area and search shape; 5) one observation of nearest-neighbour distance.

Additional methods and definition of terms are included in the text when required.

V SEXUAL DIMORPHISM IN RELATION TO FEEDING BEHAVIOUR

Bar-tailed Godwits show sexual dimorphism not only in weight (Evans and Smith 1975) but also in bill- and leg-length (Table 1). Dimorphism is most pronounced in bill-length, that of females being about 25 per cent longer than that of males. In this section I shall show that this dimorphism is associated with differences in the behaviour of feeding godwits.

1) Methods

Data were collected during both flood and ebb tides on HIS, but only during flood tides at SB as the birds were slow to return there after roosting during the high water period.

On HIS, observations were made in the same area during both flood (High water + $8\frac{1}{2}$-10 hours) and ebb (HW + 3-$4\frac{1}{2}$) tides. The godwits fed mainly on Arenicola marina which was present at densities ranging from 25.0 to 31.2 m^2. Data were collected from 40 flocks, each of between 9-32 birds. Twenty flocks (5 of females only, 7 of males only, and 8 containing about equal numbers of both sexes) were watched on the flood tide and the other 20 (4 of females only, 7 of males only and 9 with an approximately equal division of the sexes) on the ebb tide.

At SB (an unstable sea-beach exposed to the North Sea), a zonation of the major prey-species of godwits occurred in 2 of the 3 field-seasons during the early autumn months. Observations were made at the south-eastern end of the bay between HW + 7-8 when the birds fed chiefly on Nereis diversicolor and between HW + $8\frac{1}{2}$-$9\frac{1}{2}$ when they fed at higher tidal levels on Arenicola marina. At this site, Nereis and Arenicola densities ranged from 850 - 1100/m^2 and 11-16/m^2 respectively in the zone where each species predominated. Since flocks of godwits fed by walking several tens of metres back and forth along the moving tide-line, the wide local variations in Nereis densities should not be of significance. Twelve flocks were observed in the Nereis zone: 4 of females only, 4 of males only and 4

Table 1. Bill and tarsus lengths (mm) of adult Bar-tailed Godwits collected at Lindisfarne.

	Number of Birds	Bill	Tarsus
Males	39	81.0 ± 0.56	43.9 ± 0.32
Females	34	101.1 ± 0.79	48.3 ± 0.42

Figures quoted are Means ± Standard error. Bill length was measured from the feathers to the tip of the upper mandible, tarsus from the proximal end of the tibio-tarsus to the hallux.

containing about equal numbers of both sexes. Nineteen flocks (5 of females only, 6 of males only and 8 with approximately equal numbers of the two sexes) were observed in the Arenicola zone. In both zones the flocks contained 7 to 12 birds.

Observational periods of 40-80 minutes were divided into successive intervals of 10 minutes. During the first of these, the locations of birds were noted every 30 seconds, and during the second, probing and items taken/min by individual birds were measured; the sequence was then repeated. Two categories of feeding location (as previously described) were distinguished: 'at the tide-line' and 'beyond the tide-line'.

All data were collected on calm days with substrate temperatures above 3°C, as on very windy days and at lower temperatures Arenicola form casts (the cue to which godwits respond to capture this prey) less frequently.

The analyses which follow concentrate on sexual differences in feeding locations and in the probes and items taken per minute by birds feeding on the single main prey-species on HIS during flood and ebb tides and on the two principal prey-species at SB during the flood tide only.

2) Results

The data from godwits feeding on Arenicola on HIS are summarized in Tables 2 and 3. In most cases the data are analysed statistically, by Student's t-test, only for mixed-sex flocks, as most flocks observed (161 out of 200; 80.5 per cent) contained birds of both sexes.

During flood tides males showed a marked tendency to feed 'at the tide-line', whether in single- or mixed-sex flocks, while more females fed 'beyond the tide-line'. This difference was more marked in mixed-sex flocks where 21 as against 68 per cent of males and females, respectively, fed 'beyond the tide-line'. Whereas females were equally successful in obtaining prey in both locations, males probed less and were less successful 'beyond the tide-line' ($p<0.05$).

On ebb tides, both sexes fed chiefly 'at the tide-line', although

Table 2. Feeding locations of male and female Bar-tailed Godwits feeding on Arenicola in flocks of different sex ratio during the flood and ebb tides on Holy Island Sands.

	Single-Sex Flock		Mixed-Sex Flock	
	Flood Tide			
Males				
At tide-line	76%	(3480)*	79%	(5260)
Beyond tide-line	24		21	
Females				
At tide-line	44%	(2280)	32%	(4700)
Beyond tide-line	56		68	
	Ebb Tide			
Males				
At tide-line	88%	(3830)	89%	(5120)
Beyond tide-line	12		11	
Females				
At tide-line	80%	(2040)	78%	(4840)
Beyond tide-line	20		22	

*Figures in parentheses are the number of bird-observations

Table 3. Feeding behaviour of male and female Bar-tailed Godwits feeding on _Arenicola_ in flocks of different sex ratio in two feeding locations during the flood and ebb tides on Holy Island Sands.

	Single-sex Flock			Mixed-sex Flock		
	Probes/min		Items/min	Probes/min		Items/min
			FLOOD TIDE			
Males						
At tide-line	62.1 ± 3.1	(70)*	1.4 ± 0.09	62.9 ± 4.1	(54)	1.3 ± 0.08
Beyond tide-line	53.8 ± 3.3	(70)	0.9 ± 0.09	55.1 ± 3.1	(54)	1.0 ± 0.10
Females						
At tide-line	60.4 ± 2.9	(50)	1.3 ± 0.07	58.1 ± 3.5	(51)	1.3 ± 0.09
Beyond tide-line	57.3 ± 3.8	(50)	1.2 ± 0.06	57.4 ± 3.2	(51)	1.3 ± 0.11
			EBB TIDE			
Males						
At tide-line	56.4 ± 2.4	(70)	1.9 ± 0.05	56.6 ± 2.6	(56)	1.9 ± 0.10
Beyond tide-line	49.9 ± 2.8	(70)	1.7 ± 0.06	51.2 ± 2.1	(56)	1.6 ± 0.05
Females						
At tide-line	55.2 ± 3.0	(40)	2.0 ± 0.06	56.4 ± 2.8	(54)	1.9 ± 0.09
Beyond tide-line	50.1 ± 3.1	(40)	1.9 ± 0.04	51.3 ± 3.3	(54)	1.7 ± 0.10

*Figures in parentheses are the number of birds observed, each for 1 min

Note: values presented are means ± standard errors slightly more females than males fed 'beyond the tide-line' (8 and 11 per cent more in single- and mixed-sex flocks, respectively). Females were usually more successful than males but both sexes did less well 'beyond' than 'at the tide-line' (males: $p<0.01$; females: $p<0.05$ in mixed-sex flocks).

Comparison of the flood and ebb tidal situations reveals that in either sex a higher proportion fed 'at the tide-line' on the ebb. In flocks of mixed sex, 10 per cent more males and 46 per cent more females fed 'at the tide-line' on the ebb than on the flood. Additionally, on ebb tides, the birds were more successful in obtaining Arenicola. This feature is analysed more fully later (Section VII 2C).

Tables 4 and 5 summarize the data from godwits feeding on Nereis and Arenicola during flood tides at SB.

In the lower Nereis zone, a greater proportion of males fed 'at the tide-line' while more females fed 'beyond the tide-line'. This situation was accentuated in flocks containing both sexes, where 34 as against 62 per cent of males and females, respectively, fed 'beyond the tide-line'. 'At the tide-line' the two sexes were equally successful in obtaining prey, both in single- and mixed-sex flocks. 'Beyond the tide-line', however, females were significantly more successful than males ($p < 0.01$ in mixed-sex flocks).

A similar pattern held in the Arenicola zone with respect to both the feeding locations and the relative success of the two sexes. Indeed, all differences noted in the Nereis zone were further emphasized in the Arenicola zone.

Comparison of the feeding behaviour of mixed-sex flocks reveals the following points. An even lower proportion of males fed ' beyond the tide-line' in the Arenicola zone (18 per cent) than in the Nereis zone (34 per cent), while an even greater proportion of females fed 'beyond the tide-line' in the Arenicola than in the Nereis zone (70 per cent and 62 per cent, respectively). In the Nereis zone, the success rates of males were more nearly equal to those of females than in the Arenicola zone, particularly

Table 4. Feeding locations of male and female Bar-tailed Godwits feeding in flocks of different sex ratio during the flood tide in the _Nereis_ and _Arenicola_ zones of Sandon Bay.

	Single-Sex Flock		Mixed-Sex Flock	
	NEREIS ZONE			
Males				
At tide-line	60%	(1400)*	66%	(1760)
Beyond tide-line	40		34	
Females				
At tide-line	44%	(1240)	38%	(1600)
Beyond tide-line	56		62	
	ARENICOLA ZONE			
Males				
At tide-line	74%	(1920)	82%	(1720)
Beyond tide-line	26		18	
Females				
At tide-line	43%	(1520)	30%	(1560)
Beyond tide-line	57		70	

*Figures in parentheses are the number of bird-observations

Table 5. Feeding behaviour of male and female Bar-tailed Godwits in flocks of different sex ratio in two feeding locations during the flood tide in the Nereis and Arenicola zones of Sandon Bay.

	Single-sex Flock			Mixed-sex Flock		
	Probes/min		Items/min	Probes/min		Items/min
	NEREIS ZONE					
Males						
At tide-line	66.9 ± 3.9	(40)*	2.7 ± 0.05	65.1 ± 3.2	(20)	2.7 ± 0.08
Beyond tide-line	48.2 ± 3.2	(40)	2.2 ± 0.09	48.8 ± 2.9	(20)	2.3 ± 0.09
Females						
At tide-line	67.3 ± 4.1	(40)	2.8 ± 0.06	66.3 ± 3.6	(20)	2.9 ± 0.06
Beyond tide-line	63.7 ± 3.6	(40)	2.6 ± 0.07	64.0 ± 2.8	(20)	2.8 ± 0.08
	ARENICOLA ZONE					
Males						
At tide-line	62.1 ± 2.9	(60)	0.6 ± 0.09	64.8 ± 4.1	(40)	0.7 ± 0.07
Beyond tide-line	43.4 ± 3.2	(60)	0.3 ± 0.08	42.9 ± 3.8	(40)	0.3 ± 0.07
Females						
At tide-line	59.9 ± 2.4	(50)	0.7 ± 0.07	62.3 ± 4.6	(40)	0.7 ± 0.06
Beyond tide-line	57.2 ± 4.5	(50)	0.6 ± 0.04	60.5 ± 3.2	(40)	0.7 ± 0.08

*Figures in parentheses are the number of birds observed, each for 1 min

Note: values presented are means ± standard errors 'beyond the tide-line'. Here, in mixed-sex flocks, males obtained an average of 2.3 Nereis/min compared to females' 2.8/min, while in the Arenicola zone, males obtained an average of only 0.3 lugworms/min whereas females managed 0.7/min.

VI FEEDING BEHAVIOUR OF SOLITARY AND FLOCKING GODWITS

Most Bar-tailed Godwits feed in flocks. However, individuals feeding solitarily are sometimes observed. In this section, I shall detail differences in the feeding behaviour of individuals in the two situations.

1) Methods

Data were collected in the mid-tidal zone of HIS. It was possible to inspect solitary godwits for indications of injury at closer range on flood tides than ebb tides, so the data refer solely to the former situation. Observations on flocking and solitary birds feeding only 'at the tide-line' are included here,as most of the latter did not feed 'beyond the tide-line'. Data on solitary birds are comparable directly with information from individuals feeding in flocks, as measures of the feeding behaviour of the latter were obtained during the same observational periods and in the same vicinity.

Three categories of solitary birds are recognized. Sixteen godwits which were obviously injured form the first category; in most cases, these had sustained leg injuries, probably caused by stray shot. Thirty-seven godwits which left flocks of feeding conspecifics to feed solitarily, and 29 which were observed to arrive and later join a flock of feeding birds, comprise the other two categories. Observational data from these three groups are compared with those from 721 godwits from 43 flocks (7-33 birds per flock). Numbers of males and females were approximately equal in these flocks.

2) Results

Godwits in flocks probed conspicuously more often and were more than twice as successful as solitary feeders (Table 6). Of the three categories of solitary birds, those which were obviously injured did least well. Injured birds sometimes joined flocks of feeding godwits but usually did not remain for long with them. Moreover, even when they did join a flock their average intake of prey items was less than one-third of that of their

Table 6. Feeding behaviour of Bar-tailed Godwits feeding solitarily or in flocks at the tide-line in the mid-tidal zone of Holy Island Sands during flood tides with substrate temperatures above 3°C.

	Solitary Godwits			Flocking Godwits
	Injured (16)	Birds which eventually joined flocks (29)	Birds which left flocks (37)	(43 flocks - 721 birds)
Probes/min	38.5 ± 5.5	42.1 ± 4.6	41.4 ± 5.0	55.1 ± 3.2
Items/min				
Arenicola	0.2 ± 0.04	0.4 ± 0.05	0.4 ± 0.07	1.1 ± 0.06
Other	0.7 ± 0.07	0.7 ± 0.08	0.6 ± 0.09	1.5 ± 0.04

Note: numbers in parentheses are the number of birds observed
values presented are means ± standard errors

conspecifics. In contrast, the probes and intake of solitary birds which were apparently fit rose to equal those of flocking birds when they joined a flock.

Evidence from 16 birds which arrived and fed in the area in twos suggests that groups of two behave very similarly to larger assemblages. Such birds probed almost as often and were almost as successful as godwits in larger flocks, observed concurrently (53.9 ± 6.3 and 2.5 ± 0.03 as against 55.2 ± 4.1 and 2.6 ± 0.04 per min, respectively).

I have no quantitative data to indicate the distance from the nearest neighbour at which the feeding performance of an individual feeding alone became inferior to that of one in a flock, but qualitative observations suggested a distance of between 50-130 m. The area of search of solitary godwits also appeared to be less than that of flocking birds. Exceptions to this occurred when apparently fit birds left flocks. This happened most frequently around the time of low water on relatively calm, warm days; some birds then would leave a flock and often walk upshore of the tide-line. On other occasions, a bird appeared to have been left behind by conspecifics feeding actively. Such birds, sometimes 2 or 3 together, did not seem "interested" in searching for prey and were possibly satiated. Casual observation indicated that these fed at similar rates and had a similar area of search to flocking birds upon later returning to a flock.

Overall, solitary birds generally spent more time in an upright alert posture.

VII BEHAVIOUR OF GODWITS IN RELATION TO THE BEHAVIOUR OF THEIR MAIN INVERTEBRATE PREY-SPECIES

At Lindisfarne, Arenicola marina and Scoloplos armiger, two polychaete worms, are the most important prey-species taken by Bar-tailed Godwits. In this section, I shall examine the influence of various environmental parameters on the activity cycles of these invertebrates and then relate the feeding locations and the behaviour of godwits to the behaviour of their prey.

1. Invertebrate behaviour

(a) Arenicola

Wells (1949, 1957), through laboratory work, showed that Arenicola usually lies in the horizontal gallery of its U- or L-shaped burrow but makes periodic excursions to the head shaft to feed and to the surface of the tail shaft to defaecate. The horizontal gallery is generally at depths of 20-30 cm but under freezing conditions I have found Arenicola as deep as 60 cm. All these depths are beyond the reach of a godwit's bill. Thus, Arenicola are vulnerable to godwit predation only when they come to the head shaft and to the surface of the tail shaft. My initial observations indicated that godwits responded to the cue of cast formation by Arenicola to detect these, their major prey. This was confirmed later under both natural and experimental conditions (Section VII 2c). Only rarely were godwits seen to take Arenicola from the head shaft. In the study-area on HIS, densities of Arenicola ranged between 25.0 and 31.2/m^2.

I shall now discuss the frequency of defaecation by Arenicola in relation to substrate temperature, tidal cycle, and wet and dry areas of substrate in calm and windy conditions.

1) Methods

I collected data on the frequency of defaecation by Arenicola on HIS by observing simultaneously 6 selected tail shafts (indicated by casts formed within a quadrat fixed to the substrate). The times of defaecation were recorded by stop- and wrist-watches to the nearest minute. Readings of substrate temperature to the nearest 0.5°C were collected immediately before and after a period of observation and averaged to the nearest °C. After a period of observation, the worms were dug up to ensure that two or more tail shafts did not coincide. When observations were made on the flood tides the worms were dug out as soon as the tide receded. Their lengths were between about 5 and 20 cm, but no consistent differences in frequency of defaecation relative to size were found.

The frequency of defaecation by Arenicola was first examined in relation to substrate temperature, in wet areas of lower shore, in the hour before and the hour after the tide covered and uncovered the same area. Of the total number of casts formed, the numbers formed at the tide-edge were noted separately. (The tide-edge is defined as the area covered by the tide to a depth of about 15 cm, the approximate maximum depth to which a godwit may wade). On the ebb tide, the tide-edge also includes any areas of substrate which retain a thin (though decreasing) cover of water. On the flood tide the tide-edge also includes an area extending some several meters (depending on the gradient of the beach) up-shore of the advancing tide-line such that the rising water table must have flooded the Arenicola horizontal galleries.

Below a certain substrate temperature the frequency of Arenicola defaecation decreases. After this critical level had been determined, the frequency of cast formation was observed at higher temperatures, in both wet and dry areas of substrate, on both calm and windy days, and in the upper, mid- and lower shore regions. Observations in each case commenced and terminated as the tide ebbed from, and flowed over, the area at water depths of about 15 cm.

2) Results

Data on the frequency of cast formation in relation to substrate temperature are summarized and illustrated in Table 7 and Figure 2, respectively. These refer to wet areas of lower shore. For substrate

Table 7. Number of casts formed by *Arenicola* in relation to substrate temperatures in wet areas of lower shore of Holy Island Sands in one hour, as the tide covered and uncovered the areas.

No. of worm Hours	FLOOD TIDE			EBB TIDE	
	Substrate Temp. (^{o}C)	No. of Casts Formed	% Formed at Tide-edge	No. of casts Formed	% Formed at Tide-edge
60	+7	45	18 (8)	60	7 (4)
60	+6	47	17 (8)	59	7 (4)
60	+5	43	17 (7)	61	8 (5)
60	+4	46	20 (9)	60	3 (2)
60	+3	44	18 (8)	60	7 (4)
60	+2	38	43 (16)	53	7 (4)
60	+1	30	53 (16)	36	6 (2)
60	0	19	59 (11)	25	12 (3)
60	-1	7	61 (4)	13*	53 (7)
24	-2	0		0	
6	-3	0			
6	-4	0			

Note: Figures in parentheses are the numbers of casts formed at the tide-edge

*Based on 6 worm hours of observation

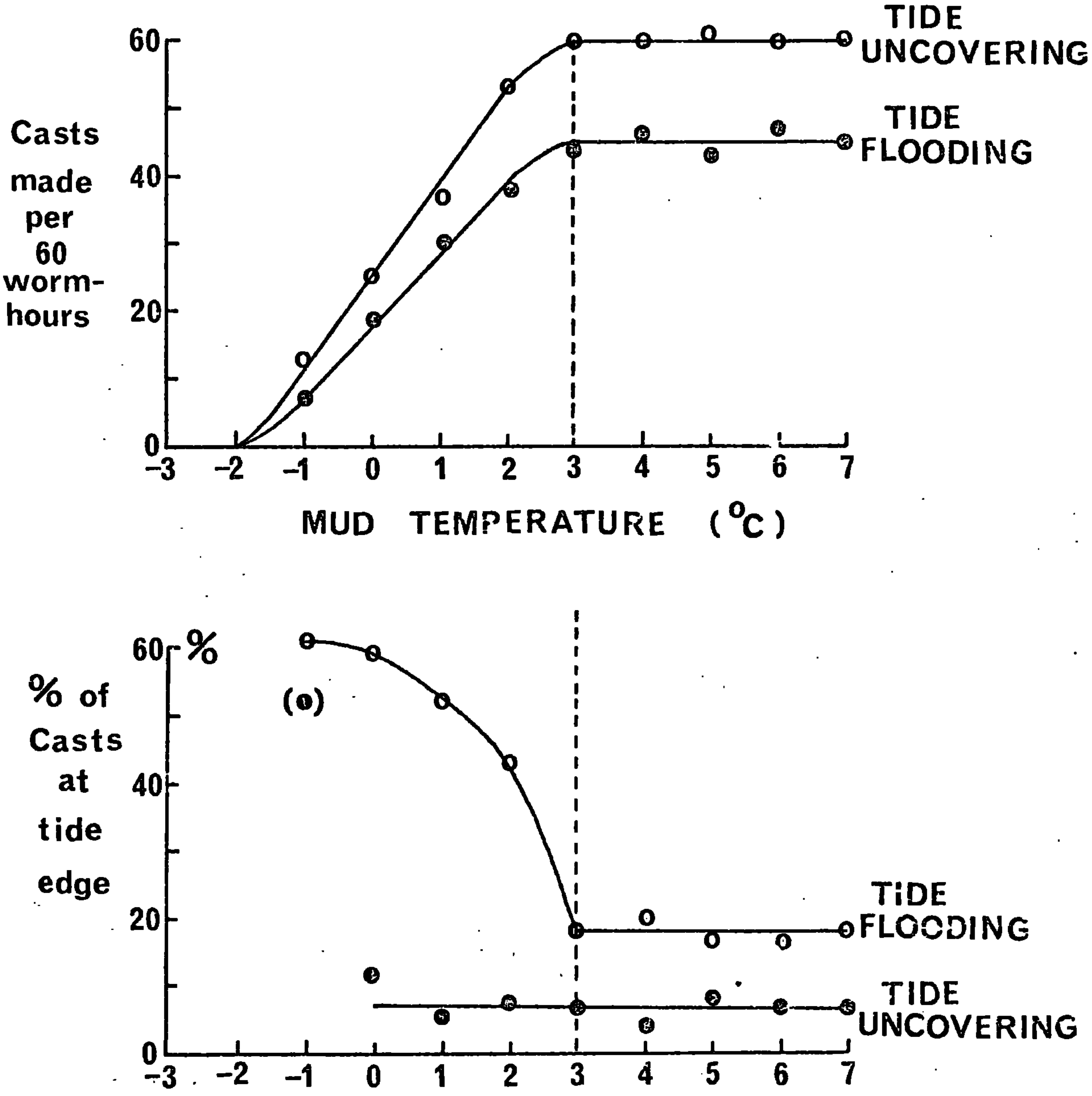

Fig. 2(a) The frequency of cast formation of <u>Arenicola</u> in relation to substrate temperature

2(b) The proportion of the casts of <u>Arenicola</u> formed at the tide-edge temperatures of -1°C and above, each set of data refers to 60 worm-hours of observation spread over 10 days. However, the scarcity of days with substrate temperatures below -1°C precluded the acquisition of equally large amounts of data for such temperatures. On flood tides, 43 to 47 of the 60 Arenicola defaecated within one hour at temperatures of +3°C and above; 17 to 20 per cent of these casts were formed at the tide-edge. At temperatures of +2°C to -1°C however, the number of casts formed decreased from 38 to 7 respectively, while those formed at the tide-edge increased from 43 to 61 per cent of the totals. No Arenicola defaecated within the one-hour observation periods at temperatures below -1°C. On ebb tides, more Arenicola defaecated than on flood tides. Within each hour, 59 to 61 casts (one worm defaecated twice) were formed by the 60 Arenicola at temperatures of +3°C, and above. Of these, only 3 to 8 per cent were formed at the tide-edge.. At temperatures of +2 to 0°C, 7 to 12 per cent of the 53 to 25 casts formed, respectively, were at the tide-edge. At -1°C, 7 of the 13 Arenicola which defaecated (53 per cent) did so at the tide-edge. All were covered by at least 2 to 3 cm of water. No casts were formed below -1°C.

In summary, more casts were formed on ebb than on flood tides at all substrate temperatures, but in both situations the rate of cast formation decreased as temperatures dropped below +3°C. The percentage of casts formed at the tide-edge as temperatures dropped increased more rapidly on flood than on ebb tides.

Table 8 summarizes data on the frequency of Arenicola defaecation at substrate temperatures above 3°C in a region of upper shore uncovered for approximately 7 hours by the tide. Cast formation by 60 Arenicola was observed in wet and dry areas of substrate on calm and windy days, respectively During gales, no observations could be made because of blowing sand.

At Lindisfarne, the extensive sandflats present a mosaic of wet and dry areas with the former usually slightly lower in elevation than the

Table 8. Frequency of cast formation by sixty Arenicola in both wet and dry areas of upper shore on Holy Island Sands at substrate temperatures above 3°C on calm and windy days during approximately seven hours in which the areas were uncovered by the tide.

CALM DAYS Mean time of Cast Formation(min)				WINDY DAYS Mean Time of Cast Formation(min)			
Wet Area	Interval[+]	Dry Area	Interval	Wet Area	Interval	Dry Area	Interval
35.2 ± 2.1		37.3 ± 2.9		38.4 ± 2.6		39.1 ± 3.1	
	47.5		56.3		57.7		88.7
82.7 ± 3.2		93.6 ± 3.5		95.9 ± 3.6		127.8 ± 3.8	
	60.7		84.3		77.2		205.9
143.4 ± 3.8		177.9 ± 3.7		173.1 ± 3.5		333.7 ± 4.1	
	92.1		135.3		105.2		(92.8)
235.5 ± 3.7		313.3 ± 3.5		278.3 ± 4.4		(426.5)	
	133.6		(108.9)		(145.9)		
369.1 ± 3.8		(422.2)		(424.2)			
	(52.3)						
(421.4)							

Note: Not all Arenicola defaecated as the tide was flooding the area to a depth of 15 cm; the figures in parentheses refer to those that did form casts. Calm days refer to those with wind speeds less than 10 m.p.h., windy days to those with speeds over 20 m.p.h. On windy days, cast formation under water could not always be observed.

[+] Interval between casts being formed

latter. However, "wet" areas do not necessarily remain so throughout the low tide period. On calm days, all Arenicola defaecated 5 and some 6 times in wet areas, whereas in dry areas all formed casts 4 and some 5 times before the tide flooded the study-area to a depth exceeding 15 cms. The time intervals between cast formation were longer in dry than in wet areas, particularly between formation of the third and fourth casts (Table 8). On windy days, Arenicola defaecated less often than on calm days, both in wet and in dry areas. But, as on calm days, the intervals between formation of successive casts on windy days were shorter in wet than in dry areas.

In the mid-shore region (uncovered by the tide for about 5 hours), observations of an equivalent number of Arenicola revealed that the pattern of defaecation was very similar to that found in the upper shore region on calm days at substrate temperatures above 3°C, in both wet and dry areas (Table 9). As before, the intervals between defaecation were shorter in wet than in dry areas and gradually increased in both areas prior to flooding by the tide. Although the mid-shore was uncovered by the tide for about 2 hours less than the upper shore, Arenicola defaecated at the same time intervals after the tide receded at both tidal levels. Thus individual Arenicola defaecated less often while uncovered by the tide at lower than higher regions of the shore.

In wet areas of the lower shore region, uncovered by the tide for about 2 hours, all Arenicola defaecated twice and some three times. The average interval between formation of the first and second casts was 45.1 min (Table 10), not significantly different from the values for the mid- and upper-shore levels.

The data collected on the frequency of Arenicola defaecation in different regions of shore under different conditions are utilized later to calculate the number of Arenicola available to godwits per unit time.

Table 9. Frequency of cast formation by sixty *Arenicola* in both wet and dry areas of mid-shore on Holy Island Sands at substrate temperatures above 3°C on calm days during approximately five hours in which the areas were uncovered by the tide.

WET AREA		DRY AREA	
Mean Time of Cast Formation(min)	Interval Between Casts	Mean Time of Cast Formation(min)	Interval Between Casts
36.9 ± 2.6		37.3 ± 2.8	
	43.3		57.8
80.2 ± 2.9		95.1 ± 2.7	
	60.2		85.1
140.4 ± 3.0		180.2 ± 3.9	
	89.2		(124.6)
229.9 ± 3.3		(304.8)	
	(71.6)		
(301.2)			

Note: Not all *Arenicola* defaecated as the tide was flooding the area to a depth of 15 cm; the figures in parentheses refer to those that did form casts.

Table 10. Frequency of cast formation by sixty _Arenicola_ in wet areas of lower shore on Holy Island Sands at substrate temperatures above 3°C on calm days during approximately 2 hours in which the areas were uncovered by the tide.

Mean Time of Cast Formation (min)	Interval Between Casts
33.7 ± 3.2	
	45.1
78.8 ± 2.9	
	(46.5)
(125.3)	

Note: Not all _Arenicola_ defaecated as the tide was flooding the area to a depth of 15 cm; the figures in parentheses refer to those that did form casts

(b) Scoloplos

Godwits appear to detect _Scoloplos_ by tactile means, while probing into the substrate. In the study-area on HIS densities ranged from 0 to 1000 and from 0 to $175/m^2$ on wet and dry areas of substrate, respectively. Preliminary investigation revealed that _Scoloplos_ were seldom found at depths exceeding 15 cm. Normally, they were found above the de-oxygenated layer or particularly concentrated empty shell-layers, even when these occurred at shallow depths. Often, high numbers were located in rotting seaweed buried just beneath the surface.

I shall now discuss the vertical movements of _Scoloplos_ in relation to substrate temperature, tidal cycle and wet and dry areas of substrate.

1) Methods

A sampler with internal dimensions of 10 x 10 cm, 25 cm deep was used to remove samples from the substrate. Slits in the sampler on opposite sides at 2 and 5 cm intervals enabled a metal slide to be pushed through so that the sample could be divided into layers corresponding to different depths. The sampler was inserted into the substrate to a depth of about 20 cm and removed with the sample. Slides were quickly pushed through the opposing sides and the top three 5 cm layers were removed and placed into separate polythene bags. _Scoloplos_ were extracted from each of the layers by sieving on the day of sampling and preserved in 70% alcohol. Great difficulty was experienced in obtaining whole worms as _Scoloplos_ tends to break during extraction and be crushed during sampling and carriage. For density estimates, only the anterior portions of _Scoloplos_ were counted.

Twenty samples (60 layers) were taken randomly (one from each of 20 1m x 1m squares on a grid) in each of wet and dry areas of substrate in the upper mid-tidal zone. Sampling commenced when the sites had been uncovered by the tide for about 4 hours. Twenty samples were also extracted both immediately ahead of the advancing flood and just behind the receding ebb tide-lines in the same wet area of substrate on the same day (a grid

Table 11. Numbers of *Scoloplos* per metre^2 at different depths in wet and dry areas of substrate and on the flood and ebb tide-lines in wet areas on Holy Island Sands at different substrate temperatures.

	Substrate Temp. +4 - +7°C				Substrate Temp. -1°C	Substrate Temp. +2°C
Depth in Substrate	Wet area (631 ± 64)*	Dry area (105 ± 38)	Flood tide-line (729 ± 73)	Ebb tide-line (684 ± 58)	Flood tide-line (547 ± 81)	Ebb tide-line (593 ± 65)
Top layer (0-5cm)	41%	36%	49%	55%	28%	43%
Middle layer (5-10)	52	56	48	39	64	52
Bottom layer (10-15)	7	8	3	6	8	5

*Figures in parentheses are the means ± standard errors of *Scoloplos*/m^2; see text for sample-sizes could not be used as I was following the tide-line). Substrate temperatures ranged from 4-7°C. Ten samples (30 layers) were collected under colder conditions at each of the flood and ebb tide-lines (substrate temperatures -1°C and +2°C, respectively). Care was exercised not to walk over the sampling locations before sampling.

2) Results

Although most Scoloplos were present in the top two 5 cm layers, differences occurred in the proportions present in these layers under different conditions (Table 11). As Scoloplos are most vulnerable to predation by godwits in the upper 5 cm, it is most relevant to compare the differences in this layer. At substrate temperatures of 4-7°C, 5 per cent more Scoloplos were present in the top layer in wet than in dry areas (both sites had been uncovered by the tide for a minimum of 4 hours). An even higher proportion were found in the surface layer in the tide-line situations, and six per cent more Scoloplos were present in the upper layer on the ebb than on the flood tide-line. These results refer to warmer (4°-7°C) substrate conditions. Under colder conditions, considerable reduction occurred in the proportions of Scoloplos present near the surface at the tide-line. Although, once again, more were present in the upper 5 cm on the ebb than on the flood tide-line, 21 and 11 per cent less Scoloplos were located there at the flood and ebb tide-lines, respectively, than on the warmer days.

Despite the high variabilities within each class of samples, which must lead to inconclusive results from statistical tests, several trends are evident. More Scoloplos are present in the upper layer (and hence are more vulnerable to predation by godwits) on wet areas of substrate at the tide-line - particularly on ebb tides and on days with relatively warm substrate temperatures. The results also show that higher overall numbers of Scoloplos are found in wet as against dry areas of substrate.

Table 12. The method of determining the Number of *Arenicola* available to Bar-tailed Godwits in relation to the area searched.

Mean density of *Arenicola*	$28/m^2$
Mean time between casts, ebb tide	47 min
Cast produced/m^2/min	28/47 = 0.595
Mean area searched by godwits, ebb tide	$10.5m^2$/min
Number of casts produced in area searched	0.595 x 10.5 = 6.25/min = approx.6/min

Note: No standard errors are attached because these would be unrealistically large, since the estimated number of *Arenicola* is obtained by multiplying three separate quantities, each of which is subject to variation

2. Behaviour of the godwits

(a) Feeding behaviour

As indicated earlier, most godwits feed in areas where their prey are most available. Arenicola defaecates at shorter intervals near the tide-edge and on wet areas of substrate than in drier areas. Scoloplos stays closer to the surface in wet areas and near the tide-edge in drier areas.

An approximate average number of Arenicola available each minute in the area searched by an individual godwit has been calculated by the method shown in Table 12. This is based on observations of the frequency of defaecation by Arenicola in the study-area on HIS and detailed previously in Tables 7 to 10.

Tables 13 to 16 summarize data on the feeding behaviour of godwits on the flood and ebb tides, and show the number of Arenicola and other prey, chiefly Scoloplos, taken per minute at different substrate temperatures in the study-area on HIS. (These data were collected in a different part of the study area and in different winters from the data on sexual differences in feeding behaviour detailed in Section V.)

Because of the sexual differences, data from males and females in each of the two feeding locations 'at the tide-line' and 'beyond the tide-line' are treated separately whenever possible. Observations were made alternately on males and females in flocks with approximately equal numbers of each sex in each of the two feeding locations. Data collected on different days for each range of substrate temperatures and for the same tidal situations were pooled before statistical analysis. The data are analysed by Student's t-tests. Other methods, terms and the sequence of observations were described earlier. Densities of Arenicola, checked frequently, were between 25.0 and 31.2/m^2.

(i) Behaviour of individuals 'at the tide-line'

At substrate temperatures above $3^{\circ}C$, males and females took significantly more Arenicola (Males: $p < 0.01$; females: $p < 0.01$), but

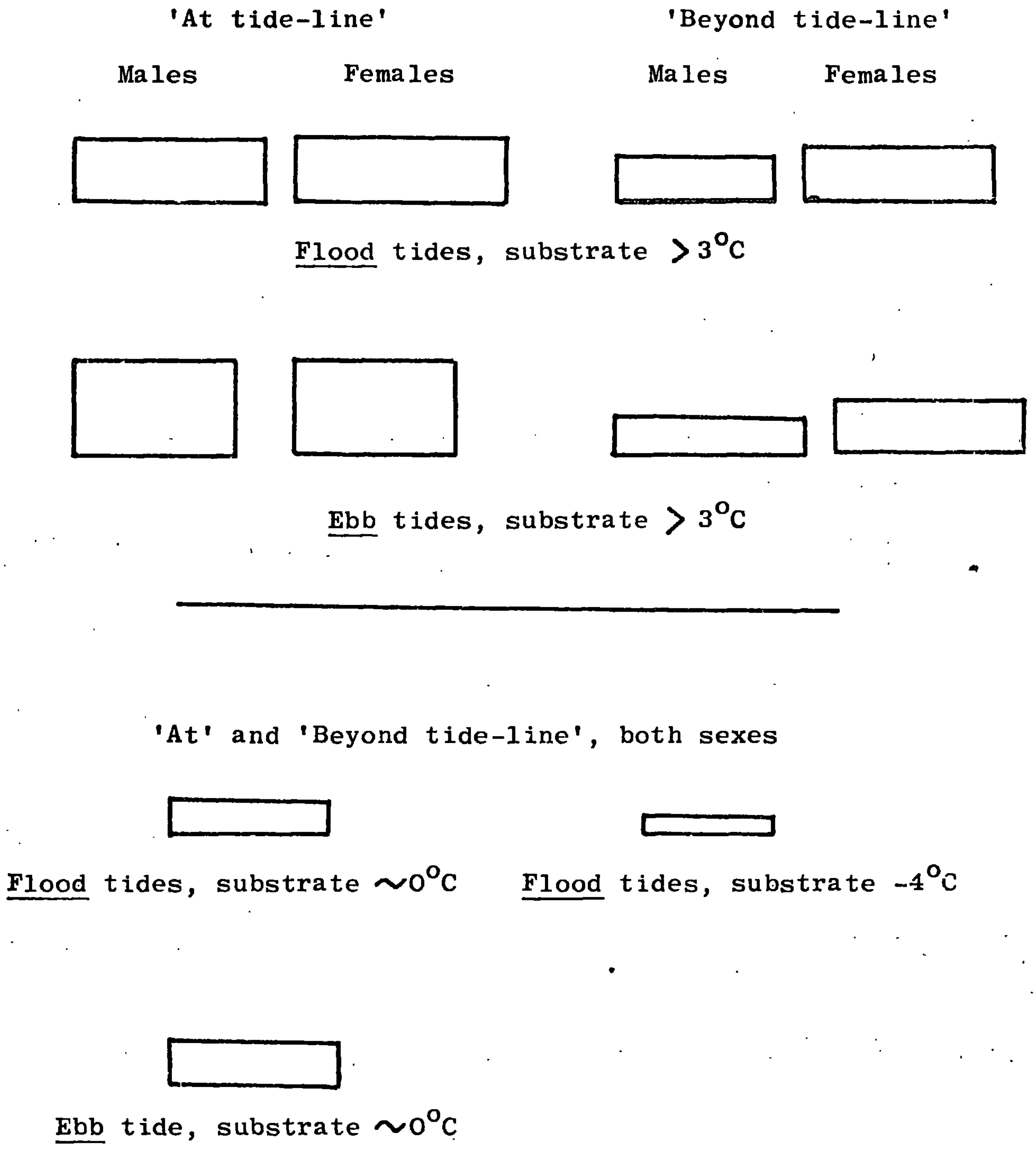

Fig. 3 Shape of search area of Bar-tailed Godwits on flood and ebb tides at different substrate temperatures

Table 13. Feeding behaviour of Bar-tailed Godwits 'at the tide-line' of the mid- and lower tidal zones of Holy Island Sands at substrate temperatures above 3°C.

		Flood Tide (21: 60 to 90)*	Ebb Tide (23: 60 to 90)
Area searched/min	males	10.51 ± 0.06m^2	11.02 ± 0.06m^2
	females	10.74 ± 0.06m^2	11.05 ± 0.07m^2
New <u>Arenicola</u> casts in area searched/min	males	6	7
	females	6	7
Probes/min	males	59.1 ± 3.4	53.9 ± 2.9
	females	58.3 ± 3.7	53.4 ± 3.4
<u>Arenicola</u> taken/min	males	1.2 ± 0.05	1.8 ± 0.06
	females	1.2 ± 0.06	1.9 ± 0.04
Other prey taken/min	males	1.7 ± 0.04	1.3 ± 0.03
	females	1.6 ± 0.06	1.4 ± 0.03
Nearest neighbour distance between godwits		2.32 ± 0.08 m	2.51 ± 0.09 m

*Numbers in parentheses refer to the number of periods of observation and the number of minutes/period; e.g. for the flood tide, there were 21 periods of observation, each of 60 to 90 min in duration. See text for the sequence of observations

Note: figures given are means ± standard errors

Table 14. Feeding behaviour of Bar-tailed Godwits 'beyond the tide-line' in the mid- and lower tidal zones of Holy Island Sands at substrate temperatures above 3°C.

		Flood Tide (21: 60 to 90)*	Ebb Tide (23: 60 to 90)
Area searched/min	Males	6.41 ± 0.04m^2	6.52 ± 0.05m^2
	Females	8.22 ± 0.04m^2	8.43 ± 0.03m^2
New *Arenicola* casts in area searched/min	Males	4	4
	Females	5	5
Probes/min	Males	53.6 ± 3.1	51.7 ± 3.6
	Females	55.2 ± 3.3	56.8 ± 3.4
Arenicola taken/min	Males	1.0 ± 0.04	1.0 ± 0.05
	Females	1.2 ± 0.05	1.4 ± 0.06
Other prey taken/min	Males	1.5 ± 0.04	1.4 ± 0.04
	Females	1.4 ± 0.06	1.4 ± 0.07
Nearest neighbour distance between godwits		1.96 ± 0.06m	2.04 ± 0.08m

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*See footnote to Table 13

fewer other prey,on the ebb than on the flood tide (Table 13). Since the other prey were much smaller than Arenicola,the godwits ingested a greater biomass on the ebb tide. Birds of both sexes searched a larger area and were farther apart while feeding on the ebb tide. The shape of the area searched by males was similar to that searched by females at all stages of tide, but differed markedly between the ebb and the flood (Fig. 3).

(ii) Behaviour of individuals 'beyond the tide-line'

At substrate temperatures above 3°C, the values for each parameter of feeding behaviour are very similar in the flood and ebb tidal situations, except that there are consistent differences between the sexes (Table 14). The shapes of the areas searched by both sexes on both flood and ebb tides were similar and elongated parallel to the tide-edge; however, that of the females was greater in width (Fig. 3).

Comparison of feeding performance 'at the tide-line' (Table 13) and 'beyond the tide-line' (Table 14) shows that while the birds took approximately equal numbers of Arenicola in both situations on flood tides, they obtained significantly fewer Arenicola (males: $p < 0.01$; females: $p < 0.05$) 'beyond the tide-line' on ebb tides,and covered significantly smaller search areas (males: $p < 0.01$; females: $p < 0.05$). However, they took a higher proportion of the Arenicola available 'beyond the tide-line' than 'at the tide-line' (e.g. on flood tides, males: 1.0/4 v 1.2/6; females: 1.2/5 v 1.2/6).

(iii) Behaviour of individuals feeding on warm and cold substrates

(a) On the flood tide

Observations are summarized in Table 15. Relatively few cold days (substrate temperatures below +2°C) occurred during the study period so the data collected on these days had to be pooled irrespective of sex or feeding location. Approximately equal numbers of observations have been included of males and females both 'at' and 'beyond the tide-line'. These data are compared in Table 15 with similarly pooled data collected on warm

Table 15. Feeding behaviour of Bar-tailed Godwits during the flood tide on warm and cold days and on one very cold day in the mid- and lower tidal zones of Holy Island Sands.

	Substrate Temp. above 3°C* (21: 60-90)	Substrate Temp. +1 to -1°C (6: 60-90)	Substrate Temp. -4°C (1: 60)
Area searched/min	8.9 ± 0.05 m²	5.34 ± 0.02 m²	2.21 ± 0.04 m²
New *Arenicola* casts in area searched/min	5	2	0
Probes/min	56.6 ± 3.4	61.5 ± 3.6	47.1 ± 4.1
Arenicola taken/min	1.2 ± 0.05	.05 ± 0.008	0
Other prey taken/min	1.6 ± 0.05	1.5 ± 0.07	0.5 ± 0.09
Nearest neighbour distance between godwits	2.14 ± 0.07 m	1.05 ± 0.08 m	.97 ± 0.07 m

*See footnote to Table 13

days and previously presented in detail in Tables 13 and 14. As may be seen, on cold days the number of Arenicola taken by the birds per minute was reduced by more than half. Although similar numbers of other prey were taken per minute on both warm and cold days, the birds ingested far less biomass on cold days. The reduction in feeding success was associated with obvious reductions both in the average distance between adjacent feeding godwits and in the size of the area searched on cold days. Although quantitative data are lacking, observations indicated that a much higher proportion of the probes made were deeper on cold than on warm days.

During my study, only one very cold morning occurred (in February, 1971) on which the substrate temperature was $-4^{\circ}C$. This was the last of three consecutive days with substrate temperatures at or below 0 to $+2^{\circ}C$. Both the substrate conditions and the birds' behaviour were so different on this morning that the data are presented in a separate column of Table 15. On that day, the sand- and mud-flats were completely frozen. As the tide flooded, frozen slush and ice were carried in with it and covered much of the tide-edge. The godwits were able to feed only on those stretches of shore which remained relatively free of ice. No Arenicola were taken (none was available since they formed no casts) and the rate at which other prey were obtained dropped to below a third of that on warm days (Table 15). There were also large reductions in the area searched and in nearest neighbour distance. Few birds fed at the water's edge and most were 'beyond the tide-line'. Females were conspicuously well out in the water. The area searched by both sexes was very elongated parallel to the shore (Fig. 3).

(b) On the ebb tide

Observations of feeding behaviour of godwits during ebb tides on warm and cold days are summarized in Table 16. As in Table 15, data are pooled, including approximately equal numbers of observations of males and females, both 'at' and 'beyond the tide-line'. As on the flood, so on the ebb tide significantly fewer Arenicola were taken per minute on cold days ($p < 0.05$); but again the numbers of other prey taken per minute were comparable with

Table 16. Feeding behaviour of Bar-tailed Godwits during the ebb tide on warm and cold days in the mid- and lower tidal zones of Holy Island Sands.

	Substrate Temp. above 3°C (23: 60-90)*	Substrate Temp. +1 to -1°C (4: 60-90)
Area searched/min	9.25 ± 0.05m²	7.86 ± 0.04m²
New *Arenicola* casts in area searched/min	6	4
Probes/min	54.0 ± 3.3	59.8 ± 4.0
Arenicola taken/min	1.5 ± 0.05	.09 ± 0.005
Other prey taken/min	1.4 ± 0.04	1.2 ± 0.05
Nearest neighbour distance between godwits	2.28 ± .06m	1.51 ± 0.07m

*See footnote to Table 13

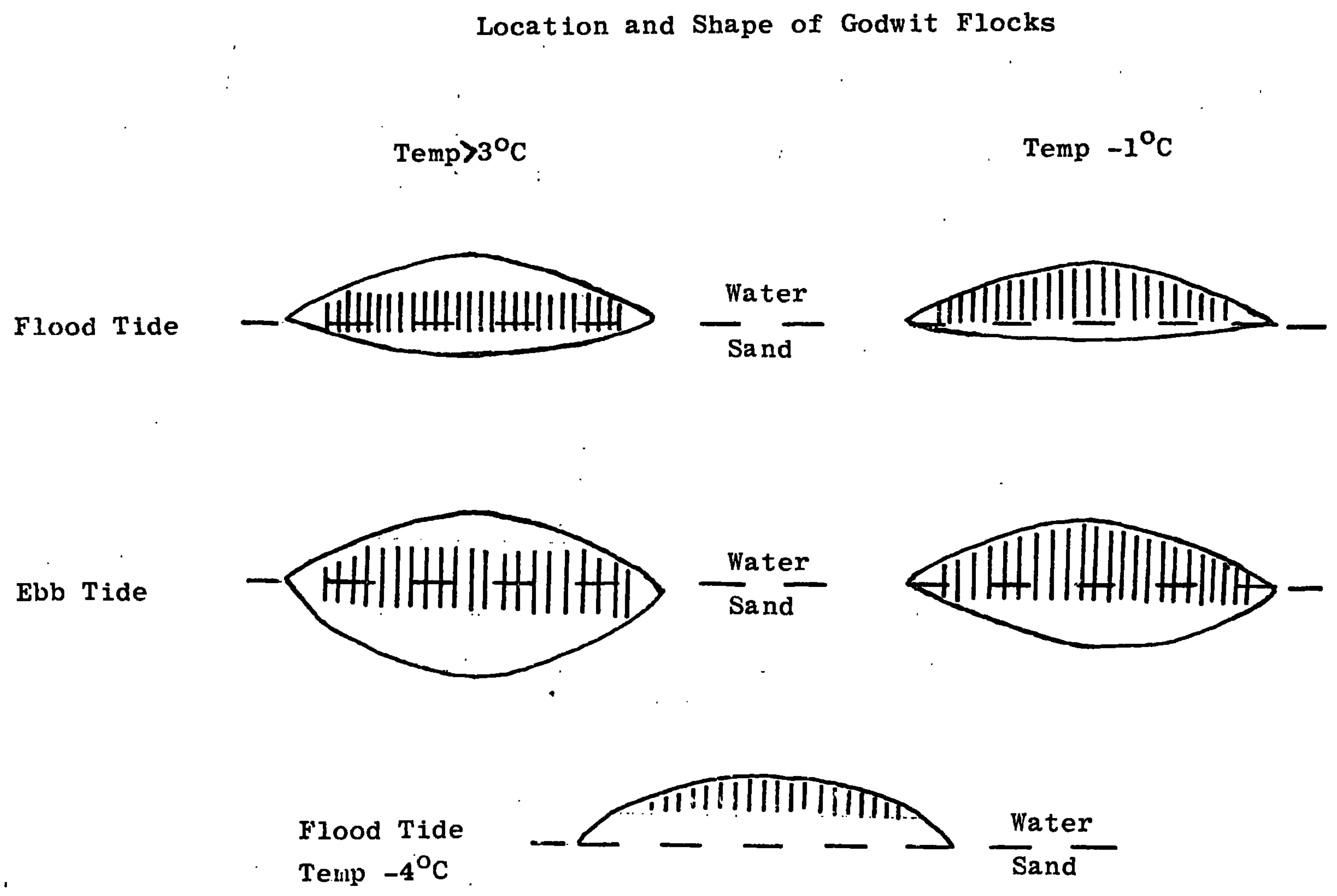

Fig. 4 Shape of flocks of Bar-tailed Godwits during flood and ebb tides at different substrate temperatures. (Shaded portions indicate where more than half of the birds were located)

those taken on warm days. On cold days, the distance between godwits was reduced considerably and the area searched decreased by almost 1.5 m^2 when compared with warm days. As noted for the flood tide situation on cold days, there was also a conspicuous increase in the proportion of deep probes,although quantitative data are lacking.

(iv) Flock behaviour

Fig. 4 illustrates the position and shape of godwit flocks in relation to the tide-line. The diagrams represent a composite picture derived from the observational methods which have been described earlier. Shaded portions of each diagram indicate where more than half of the birds were located within the flocks; unshaded diagrams indicate approximately regular dispersion of birds within the representative flock.

On warm days, the flock-shape was more elongate and the flock situated closer to the tide-line on the flood than on the ebb tide, when it tended to be upshore of the water's edge (Fig. 4). On cold days, however, most birds in the flock fed 'at' or 'beyond the tide-line', with very few upshore of the water's edge. This is reflected in the shape of the area searched by each individual (Fig. 3) and particularly in the flock-shape (Fig. 4) both of which were more elongate on cold than on warm days. This situation was not so pronounced on ebb tides,when flock-shape and location and the shape of the area searched on cold days resembled those found for the flood tide under warm conditions.

(b) Agonistic behaviour

1) Methods

The methods of collecting data on intra- and interspecific interactions on the study area of HIS and its method of presentation have been described earlier. Three categories of encounter are distinguished: those when walking, over individual feeding sites, and over prey items; a feeding site is the actual hole into which a bird is probing. Observations were made on the same days when information on feeding behaviour was obtained.

2) Results

(i) Intraspecific encounters on the flood tide

Data for warm and cold days are summarized in Table 17. On cold days with substrate temperatures of +1 to -1^{o}C the overall probability of encounter increased almost threefold over that found on warm days. However, the probability of encounter over prey items, particularly large Arenicola, once extracted from the substrate, increased more than did the probabilities of encounters when walking or over feeding sites. On the one very cold morning described earlier (Section VII 2a), the overall probability of encounter again increased almost threefold over that on the less cold days. The number of encounters involving more than 2 birds also increased. The largest number of encounters once again were over prey items, but, on the very cold morning, they did not include Arenicola. The mean distance between godwits was reduced to 0.97 ± 0.07 m (Table 15), the lowest ever observed. This must have influenced the higher rate of interaction. Interactions seemed more prolonged on cold than warm days, but it was not possible to time them while collecting, simultaneously, data on feeding rates, nearest neighbour distances, etc. On cold days females appeared to interact least, being farther out from the tide-line than males.

(ii) Intraspecific encounters on the ebb tide

Encounters on the ebb tide also increased during cold weather (Table 18) but not as much as on the flood tide. As before, encounters over prey items were more frequent than were the other forms of interaction.

(iii) Interspecific encounters on flood and ebb tides during warm days

Encounters between godwits and other species were seldom seen during the periods of observation on the study-area on HIS on warm days. Altogether, only 12 interactions with Black-headed Gulls (Larus ridibundus), Common Gulls (Larus canus) and Curlew (Numenius arquata) were noted in the 2681 godwit-minutes of observation devoted to agonistic behaviour. This gives an overall probability of encounter of .0044 per minute, combining the data for both

Table 17. Agonistic behaviour among Bar-tailed Godwits during the flood tide in the lower and mid-tidal zones of Holy Island Sands with warm and cold substrate temperatures.

	Substrate temp. above 3°C (1350)[+]	Prob. of Encounter/min	Substrate Temp. +1°C to -1°C (480)	Prob. of Encounter/min	Substrate Temp. -4°C (99)	Prob. of Encounter/min
Encounter when walking	26 [0][*]	.0192	10 [0]	.0208	10 [2]	.1010
Encounter over individual feeding site	29 [1]	.0214	21 [3]	.0437	15 [3]	.1515
Encounter over prey-item	38 [2]	.0281	51 [3]	.1062	23 [4]	.2323
Totals	93 [3]		82 [6]		48 [9]	
Overall probability of encounter		.0688		.1708		.4848

[+] Numbers in parentheses are the number of godwit-minutes observed

[*] Figures in square brackets are the number of encounters which involved more than 2 birds

Table 18. Agonistic behaviour among Bar-tailed Godwits during the ebb tide in the mid- and lower tidal zones of Holy Island Sands with warm and cold substrate temperatures.

	Substrate Temp. above 3°C (1331)[+]	Prob. of Encounter	Substrate Temp. -1°C to +1°C (395)	Prob. of Encounter
Encounter when walking	18 [0] [*]	.0135	6 [0]	.0151
Encounter over individual feeding site	21 [1]	.0157	12 [2]	.0303
Encounter over prey-item	27 [1]	.0202	25 [3]	.0632
Totals	66 [2]		43 [5]	
Overall **probability** of encounter		.0495		.1088

[+] Numbers in parentheses are the number of godwit-minutes observed

[*] Figures in square brackets are the number of encounters which involved more than 2 birds

flood and ebb tides (7 and 5 encounters, respectively). These interactions were not initiated by godwits. All but two involved encounters over prey-items when the godwits were robbed; the two exceptions were between curlew and godwits over feeding sites.

(iv) Interspecific encounters on flood and ebb tides during cold days

On cold days (excluding the most severe morning which is treated later) interspecific interaction increased about equally on both flood and ebb tides. In 875 godwit-minutes of observation from both tidal situations, 15 interactions occurred between godwits and other species, an overall probability of encounter of .0171 per min. These encounters with godwits involved Black-headed and Common Gulls, Curlew, Redshank (Tringa totanus) and Grey Plover (Pluvialis squatarola), in descending order of frequency. Twelve of the interactions were over feeding sites and, more particularly, prey-items. Godwits displaced Redshank and Grey Plover, but the larger gulls and Curlew initiated the other interactions with the godwits.

On the coldest day, with substrate temperature of -4°C, interspecific behaviour was confused. Almost all the waders and a number of gulls were feeding at the water's edge and beyond. It was impossible to note all the encounters 'while walking' which involved godwits and other species, including Dunlin (Calidris alpina) and Knot (Calidris canutus). However, in the 99 godwit-minutes observed, there were 31 encounters over feeding sites and prey-items, an overall probability of encounter of .3131 per min for these two categories.

Combining the number of intra- and interspecific encounters on this coldest morning, the overall probability of encounter for godwits, excluding the category of interspecific encounter 'while walking', was .7979 per min.

(c) Detection of Arenicola by godwits

On HIS, godwits succeeded in taking more Arenicola/min from areas just upshore of the tide-line on the ebb tide than on the flood. This might have been due to longer times between cast formation by the worms on the flood tide, but an additional or alternative factor could have been a reduction in the ease with which new cast formation would be noticed by the birds. During the ebb tide, old casts are washed away, so that casts formed on the newly exposed sand should be easily visible. On the flood tide, however, new casts are formed in a landscape already covered by casts; this might hamper the ease with which, or the distance at which, they are detectable by the godwits. To test this, an experiment was conducted at SB, a site which could be viewed from a higher elevation than HIS, so that cast formation and bird behaviour could be more accurately determined. The density of prey was, however, rather less than on HIS. The rate of cast formation by Arenicola was held approximately constant during the experiment by working only in the mid-tidal zone and on the flood tide. Ebb tide conditions were simulated by removal of all Arenicola casts from a piece of beach not more than 30 min before the tide began to flood the area. The birds' behaviour, when they returned to feed in this situation, was compared with their behaviour in the same place on the next day when all casts formed during low tide were allowed to remain. The area cleared of casts was approximately 100 m long parallel to the tide-line and 10 m wide.

The godwits, which previously had been flushed to the far end of the bay, were 'walked' back and observation began as soon as the tide pushed the birds into the experimental area. Individual birds of each sex were watched alternately for 30-second periods until the tide had covered the area. No observations were made of birds feeding on the substrate covered by the tide. The experiment was repeated 8 times during the autumns of two years and data pooled on the total number of attempts and of successful attempts made by the godwits to take Arenicola in relation to the distances moved to the casts. Distances were assessed in the field as numbers of bird-lengths and were later converted to metres, on the assumption that a godwit's length, excluding bill, is 25 cm. The results are based on 16 periods of observation, each being 19-25 minutes in duration. The number of godwits in the experimental area at one time varied from 6-14. Arenicola densities varied between years from 11.1 to 15.8/m^2.

Results

The results of the experiments are presented in Tables 19, 20 and 21. These show that (i) the median distances to which birds moved to try to take Arenicola were slightly greater on the simulated ebb tide than on the natural flood; this was true of both males and females, (ii) The median distances of movement which led to successful capture of Arenicola were also greater on the simulated ebb tide. Unfortunately, none of these differences could be established with statistical certainty, as shown by the considerable overlap of 95% confidence limits of the medians, even in the most extreme comparison.

The percentage of attempts which were successful varied with distance moved, and by inspection males or females were more successful at long distances in the simulated ebb tide situation than on the natural flood. Comparison between percentage success under the two tidal conditions, by means of a Wilcoxon signed rank test for pairs of observations at each distance, showed that males were significantly more successful on the simulated ebb than on the flood ($p < 0.05$) and females also ($p < 0.05$). It is likely that an experiment of this nature would be more conclusive if conducted on HIS, as here Arenicola densities were more than twice as high as at SB. The "background noise" provided by existing casts on the flood tide situation would be higher and detection of new casts correspondingly more difficult.

Table 19. Distances travelled by Bar-tailed Godwits in attempts to capture *Arenicola* at Sandon Bay during the flood tide.

Distance intervals (m)	Males			Females		
	No. of attempts	No. of attempts successful	Per cent successful	No. of attempts	No. of attempts successful	Per cent successful
0.25 m	19	18	95%	18	17	94%
0.50	20	19	95	19	18	95
0.75	18	16	89	18	16	89
1.00	17	13	76	18	14	78
1.25	14	10	71	15	11	73
1.50	14	8	57	13	8	62
1.75	12	7	58	14	8	57
2.00	13	5	38	11	6	55
2.25	10	4	40	12	6	50
2.50	6	1	17	9	4	44
2.75	1	0		4	1	25
3.00	0	0		1	0	
3.25	0	0		1	0	
3.50	0	0		0	0	
$\sum x$	144	101		153	109	
Overall % successful			70%			71%

Table 20. Distances travelled by Bar-tailed Godwits in attempts to capture *Arenicola* at Sandon Bay in an area simulating the ebb tide situation.

Distance intervals (m)	Males			Females		
	No. of attempts	No. of attempts successful	Per cent successful	No. of attempts	No. of attempts successful	Per cent successful
0.25 m	21	20	95%	20	19	95%
0.50	19	18	95	20	19	95
0.75	18	16	89	19	17	89
1.00	19	15	79	18	13	72
1.25	17	13	76	18	14	78
1.50	15	10	67	16	12	75
1.75	14	10	71	13	9	69
2.00	14	8	57	14	8	57
2.25	11	6	55	12	7	58
2.50	9	2	22	10	5	50
2.75	3	0		5	2	40
3.00	1	0		2	1	50
3.25	0	0		2	1	50
3.50	0	0		0	0	0
Σx	161	118		169	127	
Overall % successful			73%			75%

Table 21. Median distances travelled by Bar-tailed Godwits in attempts to capture Arenicola at Sandon Bay during the flood tide and in an area simulating the ebb tide situation.

	All attempts	
	Flood tide	Simulated ebb tide
Male	0.97 m	1.06 m
Female	1.07	1.11
	Successful attempts	
Male	0.69 (0.56 to 0.90)*	0.83 (0.66 to 1.02)
Female	0.82	0.92

Note: figures are derived from Tables 18 and 19

*Figures in parentheses are 95% Confidence limits

VIII DISCUSSION

1. Sexual dimorphism and feeding behaviour

As shown earlier, when taking Arenicola, at substrate temperatures above 3°C, male godwits are less successful if they feed 'beyond the tide-line' than 'at the tide-line'; females are equally successful in both feeding locations. In single-sex flocks, some males must feed 'beyond the tide-line', if flock shape is not to degenerate into a linear formation. However, in mixed-sex flocks, almost all males manage to avoid feeding 'beyond the tide-line', and it is left to females to use that location. How this division of feeding locations between the sexes comes about is not clear; no overt intersexual behaviour was noted at any time. Whatever the mechanism, it is clearly of advantage to males to feed in mixed-sex flocks, and most of them do so (Smith & Evans 1973). At normal temperatures there is no clear advantage or disadvantage to females to feed in either location, but, as will be argued later, it becomes advantageous to feed in deeper water in colder weather, so that 'beyond the tide-line' may be considered the normal feeding location for females.

It remains to be considered why males are less successful when feeding in deeper water. A godwit's success in obtaining a lugworm is determined by three factors: its ability to detect the prey whilst it is defaecating, the speed with which it can reach the worm, and how far down the hole it can probe.

The experiments at Sandon Bay indicate that the distances from which males will move to take a defaecating lugworm are slightly less than those found for females. Possibly the shorter legs of the males significantly affect the height from which, and therefore the distance to which, casts can be detected. In deeper water, shorter legs imply immersion of more of the bird's body; hence males are probably slower than females to move to a lugworm once they have detected it 'beyond the tide-line'. Finally, in deep water, birds must presumably strike from vertically above a lugworm tail-shaft if they are to avoid parallax and aim accurately. They usually insert their bills to full-length when probing after Arenicola, so the short-billed males have less distance in which to grab the retreating lugworm than do the females. Possibly Arenicola may be able to retreat more quickly down their burrows in deep than shallow water; if so, males would again be less likely than females to catch them. Thus, in all three stages of capture of Arenicola, male godwits in deeper water may be less successful than females feeding in the same location, and less successful than males feeding 'at the tide-line'.

The relative success of males feeding in deeper and shallower water varies with the type of prey taken. When taking Nereis, as opposed to Arenicola, males did almost as well 'beyond the tide-line' as 'at the tide-line'. (Females were equally successful irrespective of the prey-species.) Nereis may be nearer the surface when immersed, as Vader (1964) reports that, upon immersion, "they go upwards at once... and may often be observed at the surface". At the high densities of Nereis encountered at Sandon Bay, even if the godwits did not detect them visually, detection by touch should have been equally efficient in both shallow and deep water, which may explain why the male godwits did almost equally well in both locations.

The division of feeding locations between godwits in mixed sex-flocks, with the females in deeper water, may have adaptive significance in reducing competition between the sexes. This function has been attributed to sexual dimorphism in body size or bill size in a variety of species, e.g. hawks (Reynolds 1972), owls (Earhart & Johnson 1970), woodpeckers (Selander 1966), the Goldfinch Carduelis carduelis (Newton 1967) and the Carrion Crow Corvus corone (Holyoak 1970).

In godwits, it is particularly advantageous for females to feed 'beyond the tide-line' during hard weather, when, as shown earlier, feeding is critical and therefore selection intense. Under very cold conditions, several shorebird species are forced to feed along the tide-line, where intra- and interspecific encounters become common. These interactions lead to loss of feeding time, if not loss of actual prey obtained. By feeding in deeper water, female godwits are involved in less interactions than if they feed at the tide-line, since few other shorebirds except Curlew Numenius arquata can wade so deep. Although I have no quantitative data, my impression was that female godwits feeding in deeper water obtained more items each minute than males feeding 'at the tide-line' in very cold weather. Selective pressures under these conditions, for both appropriate behaviour and for morphological characters such as bill- and tarsus-length, would be strong. Whether the differences in bill-length between the sexes lead to differences in size of prey taken, I have no means to decide. For worm-feeders such as godwits, such information could not be obtained from prey remains in the gizzard, and because worms are stretched as they are extracted from the substrate, they could not be categorized into sufficiently narrow length-classes to detect any differences in sizes taken by the two sexes of godwits.

Of course, selection for bill- and tarsus-length might also occur during the breeding season, as claimed by Hale (1973) for Redshank (Tringa totanus). Bill-length may also have evolved through sexual selection as argued by Jehl (1970) for two North American sandpipers. I have no information from the breeding grounds of Bar-tailed Godwits.

2. The feeding behaviour of solitary and flocking godwits

Individual godwits feeding in flocks obtain more prey in unit time than those feeding solitarily; yet a few solitary birds may almost always be found at Lindisfarne. As detailed earlier, some of these are injured and unable to walk sufficiently quickly to maintain their place in a feeding flock as it moves along the tide-edge. However, other solitary birds are not injured, but may have just arrived in a feeding area from the roost or another feeding site, or may have just left a feeding flock. Individuals tenc to leave, or to be left behind by, a flock feeding actively under conditions when they are probably satiated, for example on warm days in autumn or spring. In view of the large amount of energy expended in obtaining food, as calculated in the earlier paper, it would seem reasonable for a satiated bird not to waste energy by keeping within an actively moving flock. However, by detaching itself from a flock, it probably becomes more vulnerable to predation by raptors.

Page and Whitacre (1975) have calculated that a single shorebird is more likely to be taken by a raptor than a bird in a flock, by a factor of 3.2:1. However, it is not clear whether the solitary birds which they saw taken were trying to feed or not. Solitary godwits, for whatever reason, spend more time in upright "alert" postures than do individuals in flocks. Although this behaviour might indicate that they are looking for conspecifics, as suggested by Feare _et al_. (1974) for solitary Rooks _Corvus frugilegus_, this explanation seems improbable for waders feeding in a very open habitat, where conspecifics are seen easily. More likely, they are looking out for predators. Satiated birds can afford to spend time doing this, while birds attempting to obtain sufficient food usually cannot. Hence it is the hungry solitary feeders which would seem most at risk from predators.

My observations suggested that when as few as two godwits fed together, they spent relatively little time in "alert" stances, and were almost as successful in obtaining prey as individuals in larger flocks. This is surprising, since information I collected at Lindisfarne from 1970-75, tabulated below, indicates that avian predators were more successful in taking individual waders from small than large flocks, though species other than godwits were involved.

These observations support those of Page and Whitacre (1975), whose more extensive data indicated that, while Merlins were more likely to obtain single small sandpipers than birds from flocks, the chance of capture also decreased with increasing flock size. These data support Goss-Custard's suggestion (1970a) that the habit of compact flocking found in many wader species is promoted by avian predation.

Predator	Wader prey species	Flock Size	Attempts made	successful
Merlin _Falco columbarius_	Dunlin _Calidris alpina_ Knot _Calidris canutus_ Redshank _Tringa totanus_	1-6	8	7
"	Dunlin, Knot	9-250	5	1
Sparrowhawk _Accipiter nisus_	As above	1-7	4	4
"	As above	15-50	3	1
Peregrine _Falco peregrinus_	Dunlin, Knot Curlew _Numenius arquata_	40-100	3	3

Since, in godwits, two birds are apparently enough to constitute a flock, insofar as feeding success and time spent 'looking around' are concerned, it is probable that predation is not the only selection pressure promoting flocking. Murton (1971a) emphasized the importance of flocking in enhancing the feeding efficiency of individuals, and claimed that predation was of secondary importance, but Lazarus (1972) took a more balanced view when he wrote that "the feeding dispersion of a species is the result of an interaction of selection pressures for minimizing predation risk and maximizing feeding efficiency". Certainly birds can enhance their feeding efficiency by copying their neighbours, as detailed by Murton (1971b), and by using their neighbours as extra pairs of eyes to look for concentrations of prey (Krebs _et al_. 1972).

3. The feeding behaviour of godwits in relation to the behaviour of their prey

Calculations presented in the previous paper indicate that godwits managed to collect approximately the same amount of _Arenicola_ each hour, irrespective of the number of hours of daylight available or the energy demands they had to meet. This suggests that they were feeding at a maximum (or optimum) rate, and that variations in energy requirements were met by alterations in the duration of feeding. To achieve this, one would expect them to feed when and where the availability of prey is greatest. The question arises whether, and if so how, they do this.

The availability of Arenicola to godwits in any given area is influenced by at least four factors: (i) the absolute density of worms in the substrate (ii) the stage of the tidal cycle (iii) substrate temperature and (iv) wind speed. The last three factors influence the frequency of cast formation by Arenicola, the cue to which the godwits respond to obtain this prey.

On Holy Island Sands, godwits fed in the areas of highest density of Arenicola, when these areas were uncovered by the tide. This was particularl noticeable about 1-2 hours after the birds had returned from high water roost. By this time, the mid-shore was being uncovered by the receding tide, including the Zostera bed on HIS. This area supports average densities of Arenicola of only $15/m^2$, the lowest densities in the mid-shore. Godwits avoided feeding on the Zostera bed even in late winter when the cover of leaves was minimal, so that the major factor affecting their choice was prey density, rather than an inability to see Arenicola casts being formed. A similar distribution of predators in relation to prey density has been reported by Goss-Custard (1970b) for Redshank feeding upon the amphipod Corophium volutator.

Within the areas of highest density of Arenicola, the zones of highest availability are those where the rate of cast formation is highest. These zones move with the advancing and retreating tide, since the worms defaecate most frequently in the vicinity of the tide-edge. On the ebb tide, casts are formed less frequently the longer a site is exposed, and the more rapidly the water can drain from it. Hence Arenicola are least available furthest from the tide-edge in areas of dry sand. Godwits feed by walking back and forth along and parallel to the tide-edge, and thus stay in the zones of highest prey availability. They also sample the entire range of tidal levels each day. Prater (1972) records that Knot also feed in wet rather than dry areas of substrate; he assumed that this was related to differences in availability of prey, chiefly Macoma balthica.

When temperatures drop below 3°C, Arenicola defaecate less often, and a higher proportion of casts are formed at the tide-edge than just upshore. Godwits respond to this situation by altering their flock-shape and concentrating their feeding at the tide-edge, and on very cold days feeding entirely in the water where temperatures are higher than on the exposed sand. Under the coldest conditions, no Arenicola are taken, and the diet consists chiefly of Scoloplos, which are apparently detected by touch. Changes in diet of Redshank have also been associated with changes in prey availability with decreasing substrate temperature (Goss-Custard 1969).

During high winds, which reduce the rate of cast-formation by Arenicola by drying exposed substrates more rapidly than usual, godwits tend to feed on lee shores, even though these may have lower absolute densities of Arenicola, or in channels where wind speed is less. They also find it more difficult to feed in the water, as casts may be washed away as they are formed, and the water is turbid, so that visibility is reduced.

It seems clear that godwits choose the sites with highest Arenicola availability by responding to the rate of cast formation. This cue is used also by Oystercatchers (Stach 1944, Hulscher 1964). Thus godwits select the most profitable areas in terms of food intake per unit time (Royama 1970) and in such areas recognize specific cues which enable them to take the most profitable prey (Tinbergen 1960). Additionally, a single godwit may watch others to see what they are taking and thus facilitate its own rate of food intake. This would accord with my observations on the feeding rates of single and flocking godwits. Facilitation could occur by copying the nature of the prey, as in the Woodpigeon Columba palumbus (Murton 1971b), or the feeding location, as in the Great Tit (Krebs et al. 1972).

Social interactions in a flock situation may not always increase the rate of food intake of an individual godwit. As mentioned earlier, at low substrate temperatures, Arenicola form no casts and are therefore not available to godwits, which take entirely Scoloplos. The rate at which Scoloplos were obtained at substrate temperatures of about $0^{\circ}C$ was only slightly less than at temperatures of over $3^{\circ}C$, when Arenicola were taken as well. However, at $-4^{\circ}C$, the rate of Scoloplos intake fell to about one-third of that at $0^{\circ}C$. It is difficult to accept that these prey were only one-third as available in the very cold conditions as at $0^{\circ}C$, since only a small proportion of them moved deeper into the substrate as temperatures fell (Table II). The reduction in food intake of godwits at $-4^{\circ}C$ must have been due in part to additional time spent in interactions, but it is probably mere coincidence that the probability of interaction at $-4^{\circ}C$ was three times greater than at $0^{\circ}C$.

Goss-Custard (1970b) suggested that increasing densities of birds in a flock would lead to increased rates of interaction and thereby reduce the time available for feeding by an individual. Also Hassel (1971) showed that, at high densities of the ichneumonid parasite Nemeritis canescens, interference between individuals reduced their searching efficiency. With the godwits, as substrate temperatures fell, birds in the flock moved closer together and reduced the area searched each minute. These would seem to be inappropriate strategies to cut down time spent in interactions, but the birds may have had little option. Under colder conditions, the areas where food could be obtained were increasingly limited, so that an individual godwit had to be prepared to pack more closely to its conspecifics if it was to obtain access to a feeding area. Furthermore, other shorebird species were also restricted to the tide-line to feed, and so aggravated the situation

It may also be argued that, once godwits were taking *Scoloplos* rather than *Arenicola*, it was no longer necessary for them to maintain such large individual distances. (When taking *Arenicola* at normal temperatures, godwits spaced themselves further apart in areas of lower prey availability.)

In view of the many and sometimes interrelated factors which affect the rate at which godwits are able to obtain their prey, it has not seemed profitable to explore the simple functional response (*sensu* Holling 1959) of the number of prey taken per minute in relation to prey density. As shown above, prey availability is the all-important feature.

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Appendix I. Composition of the diet of Bar-tailed Godwits as indicated by the contents of the oesphagus and proventriculus of twenty-four birds collected on Holy Island Sands

Godwit	Number of items and size-class								
	Arenicola marina	Scoloplos armiger	Nereis diversicolor	Cirratulidae	Olig~~a~~ochaeta	Cardium edule	Macoma/Abra balthica/tenuis	Scrobicularia plana	Tellina tenuis
1	1(II)						1(III)		
2	empty								
3	1(I) 1(II)								
4	1 tail(II)						1(III)		
5							1(II)		
6	1(II)	1?							
7	1(III)						1(II)		
8	1(II)				1??				
9				1??					
10	1(I)						1(III)		
11		1					1(I)		
12	empty								
13	1(I)		1(II)						
14		2?							
15	1(II)					1(I)			
16						1(I)			
17	1(I)							1(II)	
18			1(II)	1(II)			1(III)		
19	1 tail(II)						1(II)		1(II)
20	empty								
21							1(III),1(II)		
22	1(III)						1(III)		
23	1(I)								
24	1(I)						1(III)		
Totals	I 6	1	II 2	1??	1??	I 2	I 1	II 1	II 1
	II 5	3?					II 4		
	III 2						III 7		
	II 2 tails								
	13 whole	4	2	1	1		16 bivalves: I 3		
	2 tails						II 6		
							III 7		

APPENDIX II

Sampling of invertebrates; and attempts to measure and calculate the impact of predation by godwits on Arenicola

a) Invertebrate sampling

To obtain estimates of food intake during daylight hours, godwits were observed over the complete tidal range on HIS as the tide ebbed and flowed. A sampling program designed to acquire detailed information on the densities of the invertebrates present over this large area was impracticable and not attempted. However, the results of the invertebrate survey of HIS carried out by W. F. Miller & A. Turk (Unpublished), in May and June 1973, provided outline data on the relative abundance and distribution of the invertebrates over the entire area.

After determining that godwits take primarily Arenicola and Scoloplos on HIS, I carried out a general survey of their densities in my study area on HIS. Results, expressed as average numbers/m^2 are reported elsewhere. The methods were as follows.

Scoloplos: Two samples at each site were taken at 50 m intervals along a transect from high to low water marks. The procedure was repeated along a second transect, parallel to and 50 m from the first. A 10 x 10 x 20 cm (deep) corer was inserted into the substrate and withdrawn with the sample, which was transferred intact to a polythene bag for carriage. Samples were seived, using 1 mm mesh, and Scoloplos pickled in 70% alcohol for counting at a later date. Flotation techniques, such as that described by Kajak *et al*. (1966) were tried, and proved efficient but too time consuming for use with large numbers of samples. Sampling was undertaken in early October of both 1971 and 1972. Results were combined.

Arenicola: Estimates of the numbers of Arenicola/m^2 were obtained by counting their casts. Although Newell (1948) reported this method to be unreliable, I have found it gave accurate information on numbers present provided that casts were not counted on cold days or until several hours after the area had been uncovered by the tide. My data indicated that *Arenicola* on HIS form casts at regular time intervals, so there is no reason to suspect that most *Arenicola* had not defaecated when I sampled the study area 4-5 hours after the tide had receded. Underestimation can result, however, when 2 or more casts coincide. To correct for this, 15 $\frac{1}{2}m^2$ areas were dug out to a depth of 40 cm (since under warm conditions most *Arenicola* are found at depths not exceeding 30 cm) and the extracted sand searched for *Arenicola*, after casts had been counted on the surface. The results are presented in Fig. 1 and were used to correct the cast counts made during regular sampling. In October of 1970, 1971 and 1972, casts were counted in each of two $^1/_4$ m^2 quadrats at intervals of 50 m along two transects, 50 m apart, running from high to low water mark through my study area on HIS. Corrected average numbers of *Arenicola*/m^2 are given in the text. For the determination of the number of *Arenicola* available/m^2 within the areas searched by godwits, counts of casts were made where the godwits fed.

b) Estimation of the impact of godwits on *Arenicola* and *Scoloplos* populations

1) Direct methods

Exclosures, consisting of wooden frame supports completely covered on the top and sides with chicken wire, were utilized in an attempt to make estimates of the numbers of *Scoloplos* and *Arenicola* removed by waders during the winter months. Each exclosure covered an area of 5 m^2.

Two exclosures were placed in the mid-tidal zone at the periphery of my study area in October 1971 and again in 1972. Two "control" areas of 5 m^2 were located about 100 m away from the exclosures. The numbers of *Arenicola* casts were counted in each of the exclosures and control areas at the time of placement. At the same time, 10 x 10 x 20 cm (deep) samples of substrate were collected for measurement of *Scoloplos* densities in equivalent sized areas, 10 m away from each exclosure and control area to

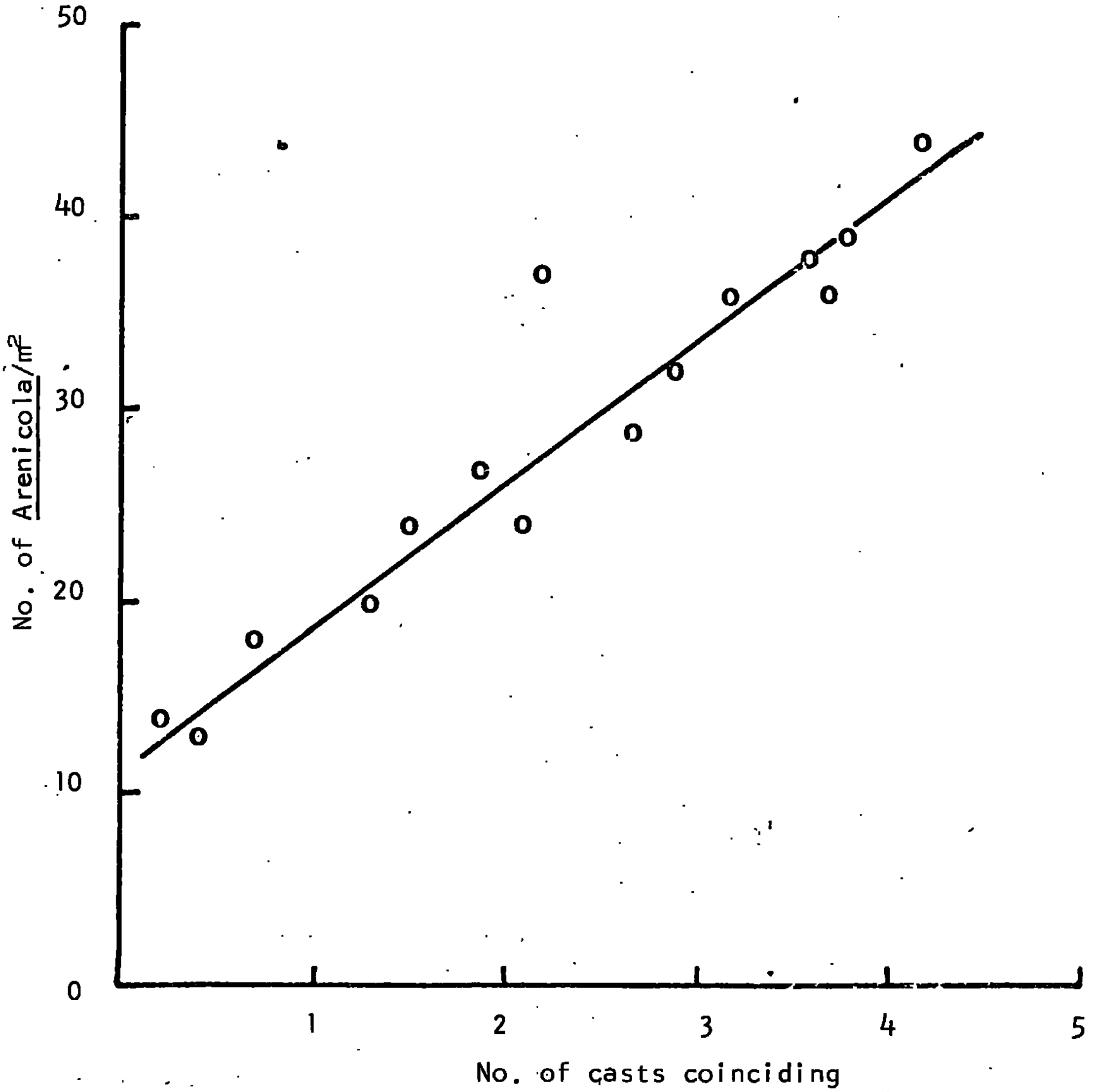

Fig. 1 Overlap of Arenicola casts at different lugworm densities

avoid disturbing the substrate within the exclosures. The following March, the numbers of casts of *Arenicola* were counted and 10 samples of substrate were collected from within each exclosure and control area. The densities measured in October and March were then compared to reveal any losses which might have been due to predation.

Results The results proved inconclusive for both *Scoloplos* and *Arenicola*. There were considerably fewer *Arenicola*/m^2 inside the exclosures than outside, perhaps becuase the wire around the base of the exclosure caused hollowing out of the substrate along the sides, and because of the growth of *Enteromorpha* spp. on the wire in February and March. There was a 4 per cent reduction in density of *Scoloplos* in the first winter and a 7 per cent increase in the second when exclosures and control areas were compared.

Results from the use of exclosures are likely to be inconclusive when they involve invertebrate species which are capable of movement during the non-reproductive season. This has been shown by Goss-Custard *et al*. (1974) with *Macoma*. Vader (1964) reported that *Scoloplos* were capable of moving horizontally through the substrate, while *Arenicola* may undertake movements downshore in cold weather. I noted, through casual observation, that the number of *Arenicola* in the channels and lower tidal areas had increased during the very cold spell in February 1971. Results from exclosures for sedentary species (e.g. *Lanice*, Goss-Custard (1974); or Cockles, Hancock & Urquhart (1965)) are likely to be more reliable.

2) Indirect method

As the results from my exclosure studies cannot be relied upon, I have attempted to calculate the impact of godwits on *Arenicola* on the basis of the average number of *Arenicola* taken by a godwit each day. Information on the distribution and densities of *Arenicola* on Holy Island Sands at the end of the winter season was obtained from a survey in May 1975, made by counting casts.

Other species, e.g. Curlew, Oystercatcher and Grey Plover, often take

Arenicola, as may flatfish. As numbers of the three avian species on HIS are small, their effect is probably not appreciable.

The calculations are as follows. The total number of godwit-days at Lindisfarne in winter 1974/75 was 531,500. Of these, 47% of feeding time was spent on Holy Island Sands, so godwit predation on lugworms there is equivalent to that exerted by 249,790 godwit-days. On average, a godwit takes 238 Arenicola each day, so that 238 x 249,790 = 59,450,020 lugworms must have been removed from Holy Island Sands during the course of the winter. By May 1975, there remained on HIS 161,558,425 lugworms, divided almost equally between 230 ha of high density ($32.7/m^2$) and 440 ha of medium density ($19.9/m^2$). Hence the autumn population of lugworms must have been at least 221,008,445, of which the godwits removed about 59 million, i.e. 26% at maximum.

It should be mentioned that other areas of the Lindisfarne Reserve also held Arenicola in May 1975, to the extent of about 65 million, chiefly in 260 ha of medium density ($19.9/m^2$) and 190 ha of low density ($6.4/m^2$).

APPENDIX III

Studies of shorebirds at Lindisfarne, Northumberland

2. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit

P. R. EVANS and P. C. SMITH

Introduction

In a pioneer study on Canada Geese, Hanson (1962) investigated possible parameters which could be used to evaluate the "condition" of migrant waterfowl during the course of their annual cycle. He studied variations in total body weight, in weights of pectoral and tibiotarsal muscles, and in weights of liver and total body fat. He concluded that no parameter could measure "condition" adequately, and, in particular, that it should not be assumed that the heaviest birds are in the best condition.

Since definitions of condition are lacking from most papers which have mentioned the subject, we begin with the assumption that condition is a measure of the chances of survival of an individual at a particular time of year, or of its potential for breeding successfully. It should, therefore, be quantifiable by examining the size of a bird's reserves of fat, protein and other groups of biologically important chemicals, in relation to the size of the demands likely to be made on these reserves at the particular time of year or stage in the annual cycle. In practice, the size of the demands may be hard to predict from armchair reasoning, but instead may be assessed by measuring the normal levels of reserves carried by birds at different times of year. These normal levels are presumed to have been selected during the course of evolution as those maximizing the chances of survival of the individual, or, indirectly, of its offspring. Condition, it should be stressed, is a relative measure, and no absolute value of a physiological or chemical parameter can indicate it. For example, a low level of body fat may indicate a bird in poor condition in mid-winter (when fat reserves "need" to be high as a safeguard against high energy demands or poor feeding conditions) but in good condition in mid-summer when high fat reserves are not needed.

This paper presents data on the body composition of 169 Bar-tailed Godwits collected at Lindisfarne during the years 1970-1975 in connection with studies on food selection and heavy metal accumulation by this species. (Birds collected between February and August, inclusive, i.e. outside the official shooting season, were obtained under licence from the Nature Conservancy Council.) In this paper, we seek to establish the normal levels of fat and pectoral muscle in birds of different size at different times of year, and to identify those stages of the annual cycle or situations in which birds find it difficult to maintain good condition. We attempt to relate these to the feeding ecology and behaviour of the godwits, as described in part in an earlier paper (Smith and Evans 1973) and in further detail here. The reader is referred to our earlier paper for a general description of the study area and its importance as a wintering area for godwits.

Bar-tailed Godwits vary considerably in size and weight, both within one sex and between sexes; smaller variations may occur with age. Data from small samples of birds collected on different days throughout the non-breeding season are thus inadequate to establish the patterns of weight change occurring within a whole population. Not surprisingly, therefore, our measurements from Lindisfarne godwits show no clear-cut trends in total body weight during the autumn, winter and spring. Similarly, data from the Wash, East Anglia, summarized by Minton (1973), suggest that there was no appreciable change in the mean weights of males or females between early autumn and winter - but winter samples were small. Even if true, important reciprocal changes could occur in the weights of certain body components, without changes in the total weight of a bird, and it is these which are explored in this paper.

Methods

Birds were collected during daylight hours, 1-2½ hours before the time of high tide, usually as they were flighting from their feeding grounds to their high tide roost. Since shorebirds feed at times mainly dictated by the tidal cycle and not by the alternation of day and night, the day-to-day condition of birds should be most comparable when considered at similar stages of the tide, rather than at the same hour of the day.

Immediately after collection, each bird was weighed and the gut removed and stored in 70% alcohol for subsequent analysis. Measurements were taken of the lengths of the bill and tarsus, and the sex was determined by dissection. The carcass was then stored in deep-freeze and eventually transported to Durham. While the carcass was thawing, the bird was aged by plumage characteristics (see later) and details of wing moult recorded. The breast muscles from the right side of the bird (the pectoralis, supracoracoideus and coracobrachialis) were excised after removal of any superficial covering of fat. They were then dried, weighed and extracted with petroleum ether (60°-80° b.pt.) in a Soxhlet extractor. The residual weight after further drying was taken to be the lean dry weight of the pectoral muscle. The liver was also removed and subjected to similar procedures, but the results are not discussed in this paper, since, as Hanson (1962) pointed out, the liver is an indicator of shifts in metabolic processes rather than of body condition.

The remainder of the carcass (i.e. minus gut, liver and one set of pectoral muscles) was also dried and fat was extracted from it by repeated washings in petroleum ether for three days. After further drying, the carcass was reweighed. The total weight of fat carried by the bird was then calculated, after due allowance had been made for fat extracted from liver and muscles. In the results discussed later, total body fat is expressed as a percentage of total body weight (including fat), termed the Lipid Index. This follows the usage of King and Farner (1966) and is the ratio appropriate for the calculation of potential flight range for a given quantity of fat (Pennycuick 1969). It is not wholly appropriate for calculation of potential survival time, however, since this is a function of a bird's metabolic rate, which varies with body weight to the power of $^3/_4$, i.e. large birds require less energy per unit weight to stay alive than do small birds. To survive a certain time, therefore, the larger female godwits require somewhat lower lipid indices than the smaller males. This difference may be enhanced further if the metabolic rate of females is lower than that of males of the same size, as has been claimed for certain other bird species (references in Hanson (1962)).

Lean dry weight of the pectoral muscles is expressed as an index related to the dimensions of the parts of the skeleton to which the muscles are attached. The area of attachment is determined by the areas of the keel and the bony raft of the sternum, together with the extension provided by the coracoid bone (Fig. 1). Although an index of muscle size could be calculated by dividing muscle weight (which should be proportional to muscle volume) by the area of attachment, such an index would not be dimensionless, and so would be unsuitable for comparison of the conditions of muscles from birds of different size. Accordingly, muscle weight for each bird is expresse as a fraction of the volume of a muscle of standard shape attached to the appropriate area, as measured for that particular bird. The standard shape was chosen after examination of the pectoral muscles of several shorebird species, and so should have correspondingly wide applicability. The standard volume for the muscle, on either side of the bird, is given by the formula

$$V = b\ (ad + 0{\cdot}433\ c^2)$$

where a = length of the sternum
b = height of the keel of the sternum
c = distance from the keel to the end of the coracoid
d = width of the bony raft of the sternum

These dimensions are illustrated in Fig. 1.

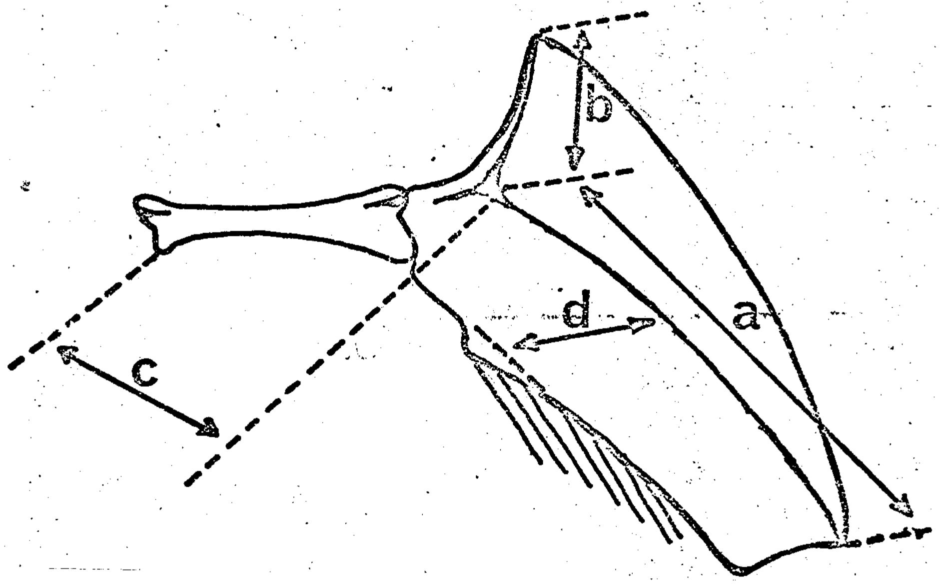

Fig. 1 Skeletal measurements used to calculate the area of attachment of the pectoral muscles and hence a standard muscle volume. For further details, see text.

Another muscle index is also used: the total lean dry weight of the pectoral muscles on both sides of the bird expressed as a proportion of the lean weight (total body weight minus fat) of the whole bird. (This index will not change if alterations in muscle size are accompanied by corresponding changes in water content of the body.)

It had been intended to present data also on the fat content of the pectoral muscles, but estimation of this quantity is unreliable when determined from whole muscles, since adhesion of even small quantities of superficial adipose tissue can produce unrealistically high values of the fat content of the muscle. Many of the determinations made on whole godwit muscles probably were free from this source of error, and in general the fat contents of muscle appeared to parallel closely the corresponding Lipid Indice for the whole birds, so they are not discussed further.

Age determination

The plumages of Bar-tailed Godwits were described in detail by Chapman (1907). Young birds arrive in August and September in warm brown "speckled" plumage, with a strongly barred tail. Later they moult their body feathers to an ash-grey winter plumage of similar colour to that of adults. However, we noticed that they retain the finely-barred tail feathers, which differ markedly from the broadly-banded central tail feathers of the adults (Fig. 2). By this feature, we were able to distinguish first-year birds from adults throughout the winter. In summer, according to Chapman, very few first-year birds acquire the red breast and belly feathers of the adults, so they may be distinguished also at this time of year.

The grey first-summer birds moult completely in late summer and early autumn, and then become indistinguishable from older birds in non-breeding plumage. At Lindisfarne, moult of the primary feathers usually was completed in late October or early November, but a few individuals were about to finish feather growth in mid-September in 1974. These may have been immature (first-summer) birds which had spent the summer months in England.

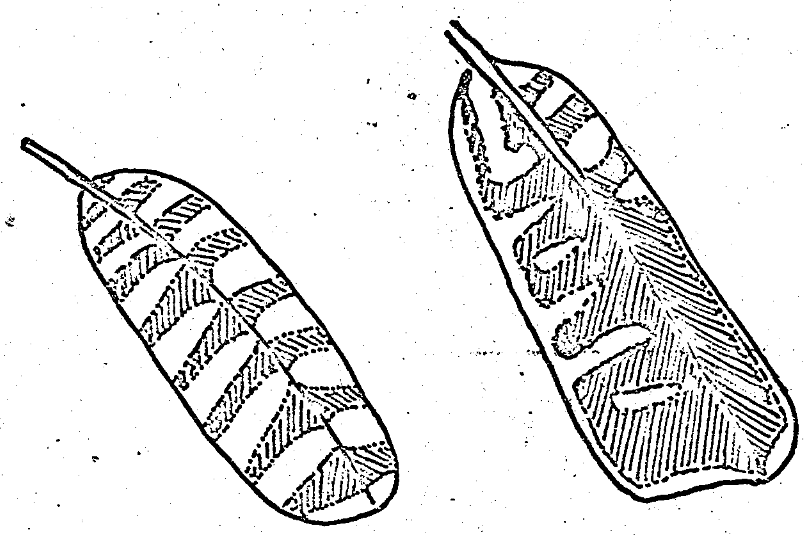

Fig. 2 Central tail feathers of juvenile (barred) and adult (banded) Bar-tailed Godwits in mid-winter. When spread, the tail feathers of adults show a terminal band.

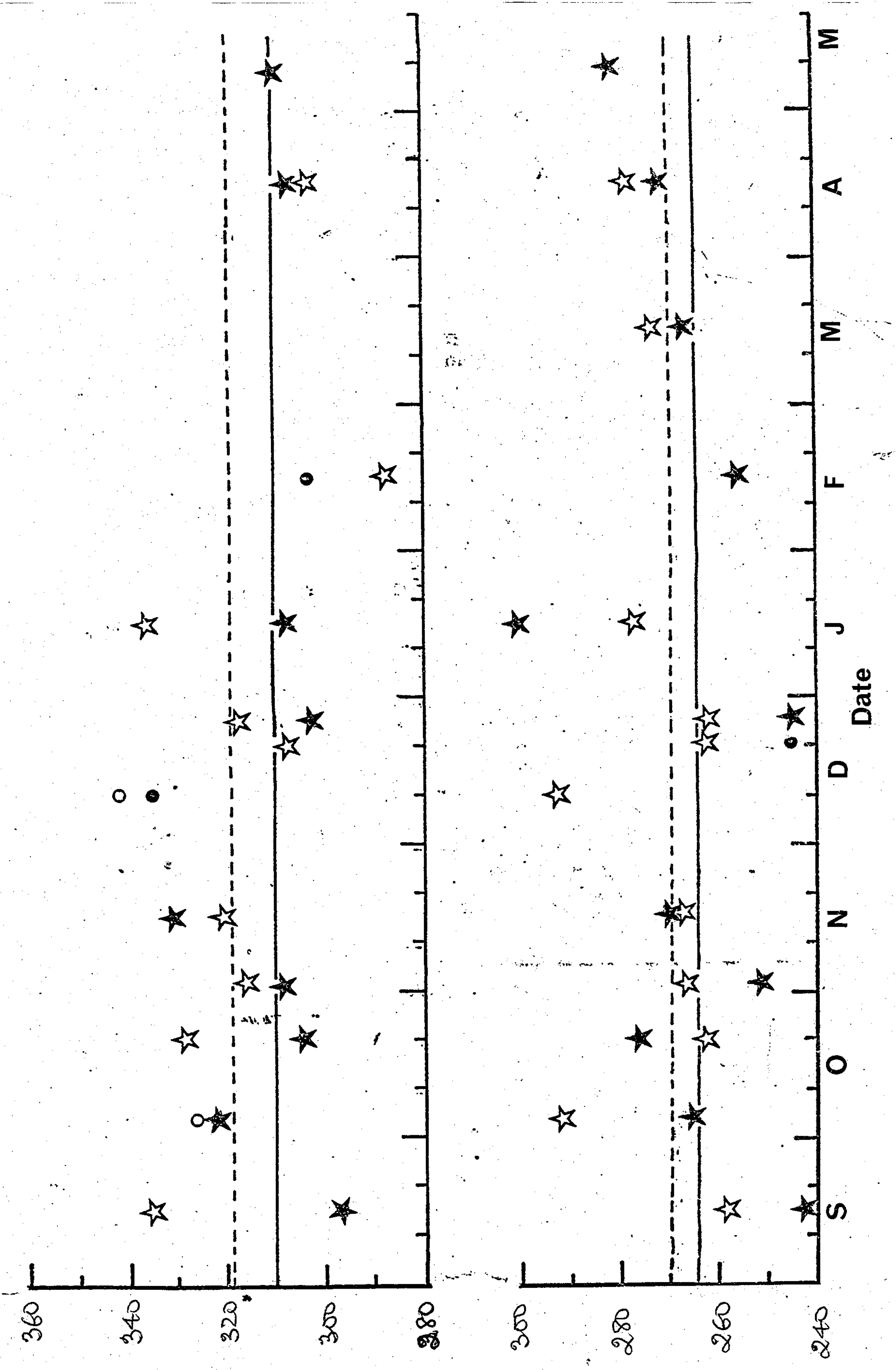

Fig. 3 Average lean weights of female (upper panel) and male (lower panel) Bar-tailed Godwits throughout the non-breeding season at Lindisfarne. Filled symbols = juveniles, open symbols = adults, large stars = mean values, small circles = single observations. Trend lines: solid = juveniles, dashed = adults.

Results

Lean weights

It had been hoped that, although total weights of godwits were very variable, even within one sex and age-class at any chosen time of year, lean weights might have been less variable, so that seasonal changes could have been detected. However, variability in body size is so great (about 15% on either side of the mean) that any trends in lean weight that might have been present were effectively swamped (Fig. 3 and Appendix I). On the few occasions when weights differed significantly between one sampling period and the next, these differences resulted from size differences in the birds examined, rather than from true weight changes in the whole population from which the birds were sampled.

On average, females were about 20% heavier than males (mean weights throughout the non-breeding season: 319 g and 270 g for adults, and 311 g and 264 g for first-year birds, respectively).

Although lean weights apparently did not change with season or physiological state, the great variability in weights could mask underlying trends in the weights of components which together make up lean weight, namely muscle, water and skeleton. (The last-named is unlikely to alter much.) No direct measure was obtained of body water, since the gut of each bird was removed before the carcass was dried. However, relative changes in the two muscle indices enable changes in body water levels to be deduced, as will be shown later.

Normal patterns of change in lipid and muscle indices during the non-breeding season: birds in "good condition"

Trends in the three indices are summarized in Fig. 4 and detailed in Appendix II. In most instances, all values for a particular index at any chosen date or period of the year were similar, and approximately normally distributed about the mean value illustrated in the diagrams. (Differences between males and females, and between birds of different sizes, disappeared

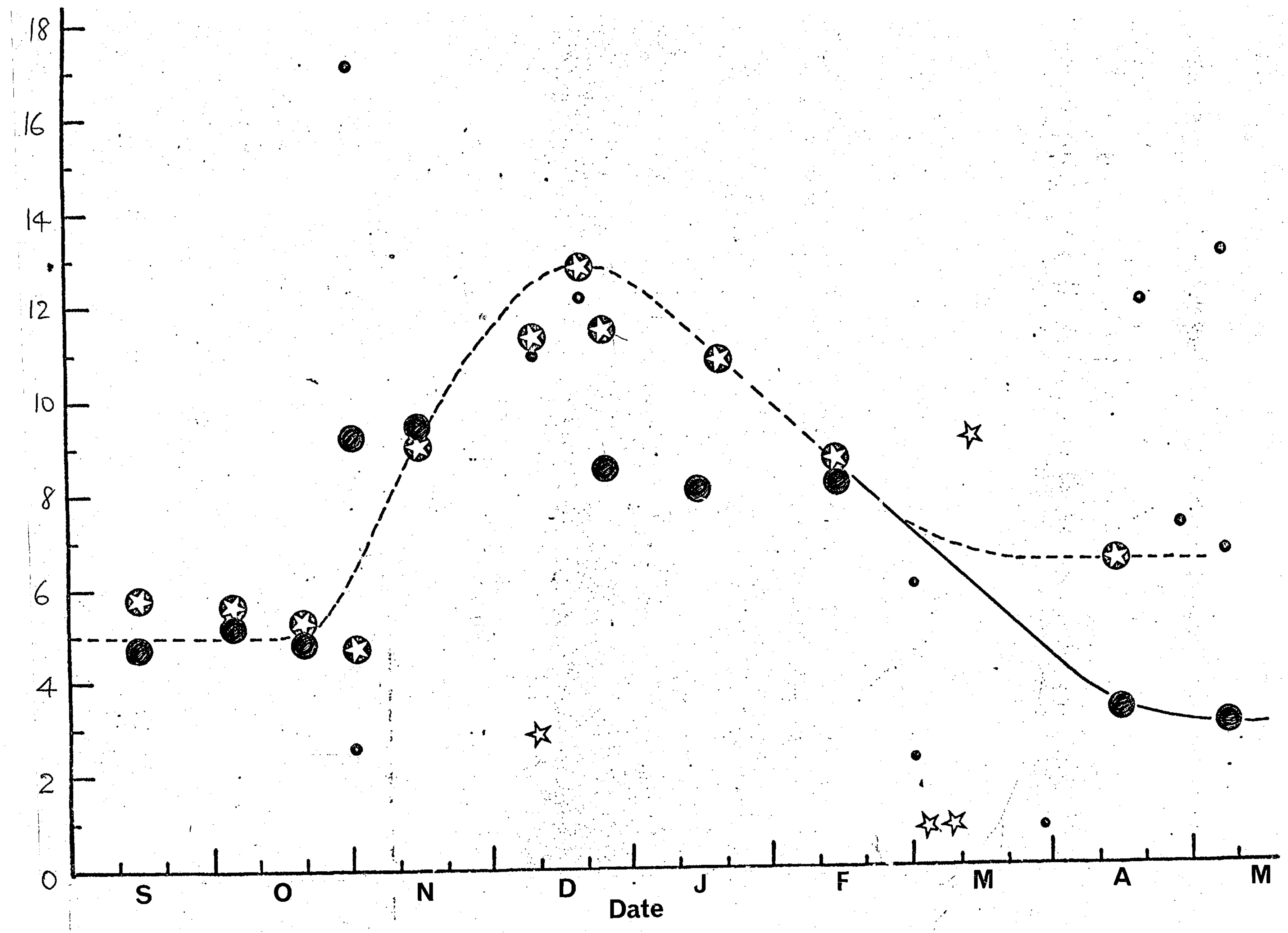

Fig. 4 (a) Lipid Indices (fat as a percentage of total body weight) of juvenile and adult Bar-tailed Godwits at Lindisfarne. Trend lines (fitted by eye): solid = juveniles, dashed = adults. Symbols: filled circles = juveniles, circles with stars = adults. Small symbols indicate data from single birds.

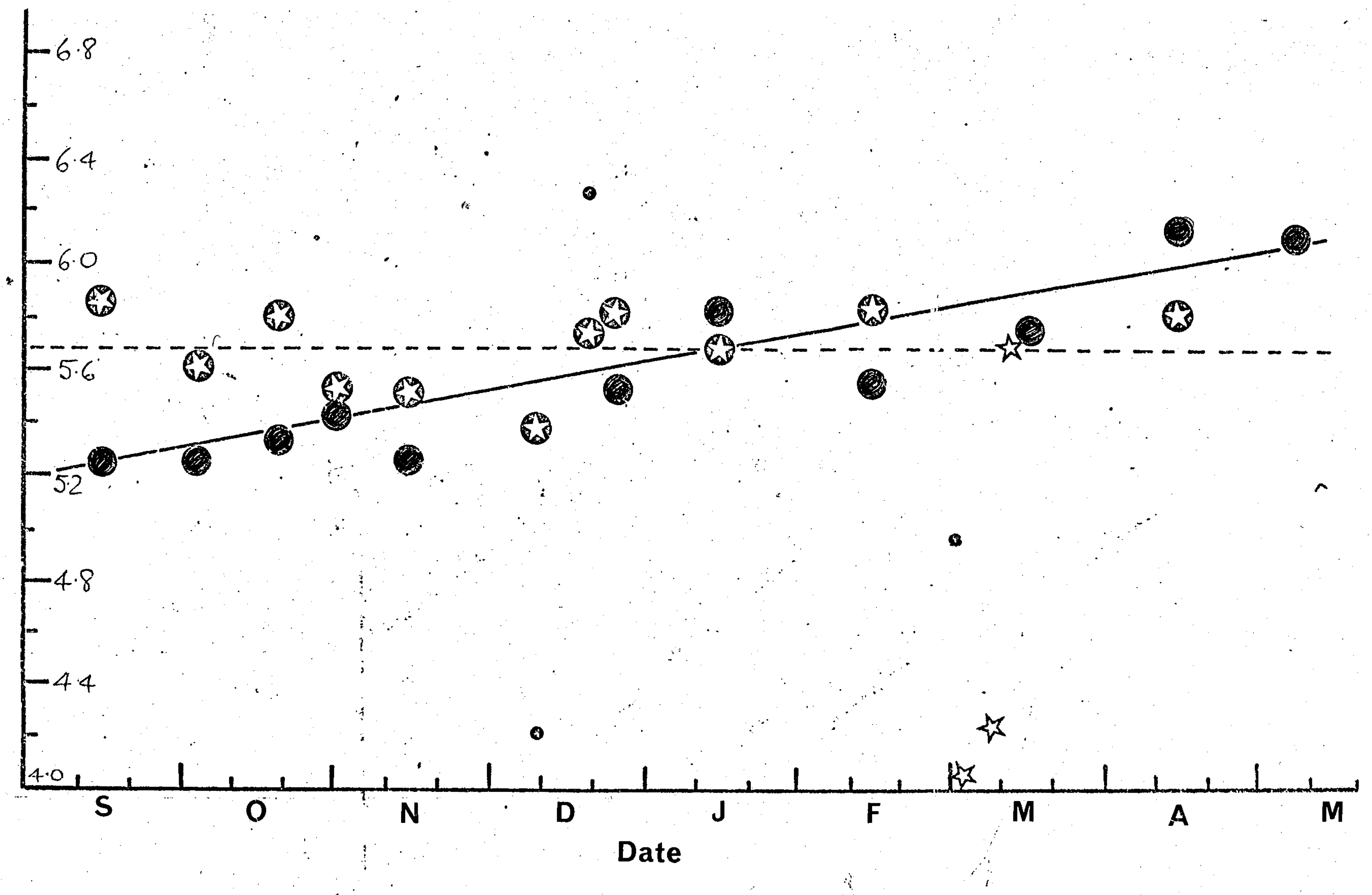

Fig. 4 (b) Pectoral muscle weight (as a percentage of lean weight) of juvenile and adult Bar-tailed Godwits at Lindisfarne. Key as in Fig. 4(a).

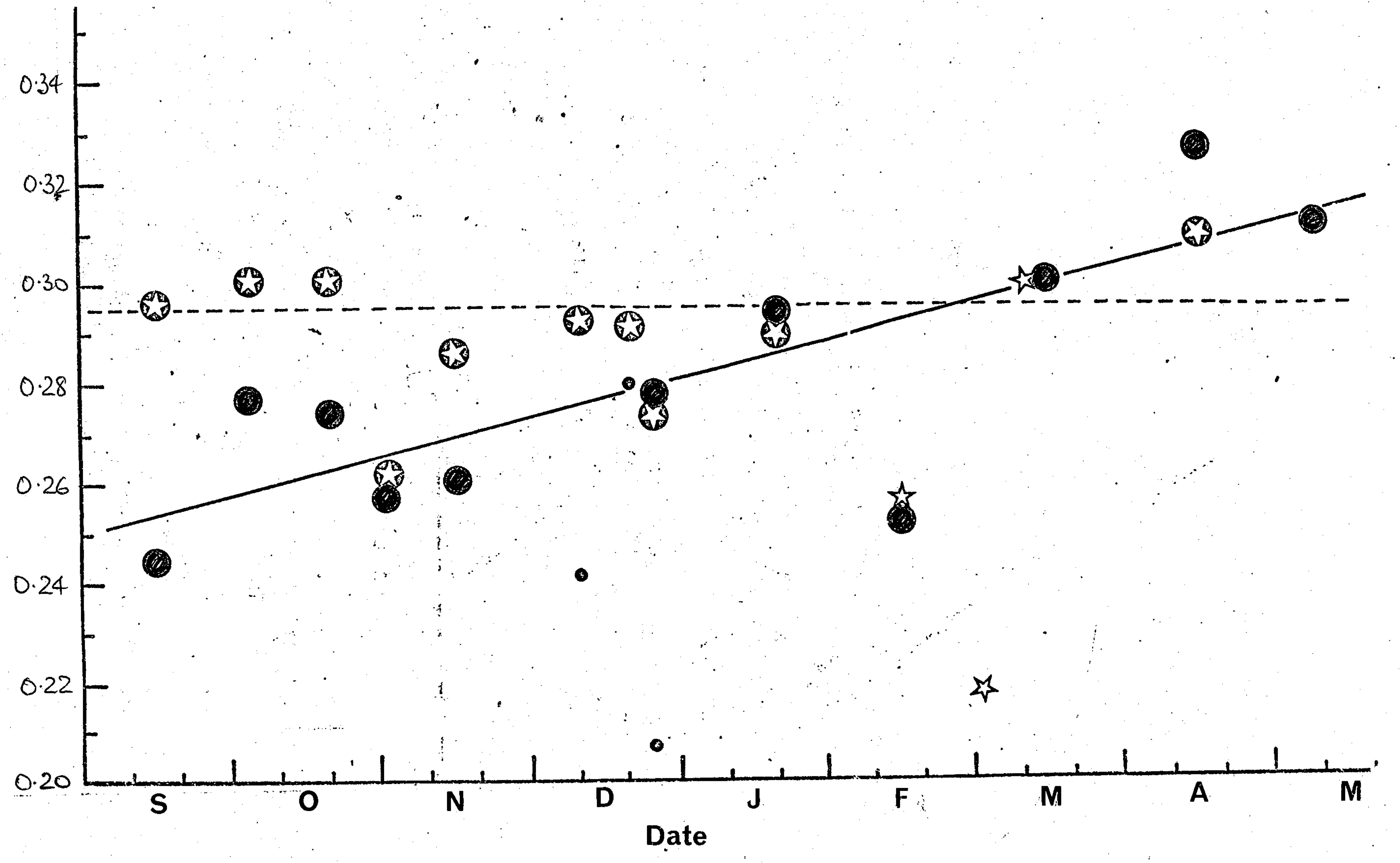

Fig. 4 (c) Pectoral muscle indices (measured in relation to standard muscle volume - see text) of juvenile and adult Bar-tailed Godwits at Lindisfarne. Key as in Fig. 4(a).

when the weights of fat and muscle were expressed as indices.) On a few occasions, exceptionally high or low values were recorded; these are shown separately in the diagrams and were excluded from calculations of the means given in Appendix II. The trends in all years were similar, so data from several years have been combined for each period of the year.

As may be seen from Fig. 4, the Lipid Indices of both adults and juveniles remained steady at about 5% during September and October, rose to a peak of just over 12% in mid-December but then fell again during the spring. By contrast, both of the pectoral muscle indices showed no change in adults throughout the winter, but a steady increase in juveniles from autumn to spring. For a juvenile of fixed skeletal size, its pectoral muscles increase in weight by about 25% between September and May, as the muscle index rose from about 0.25 to 0.31. In the same period, the proportion of the lean body weight formed by dry pectoral muscle rose from about 5.2 to 6.1%, a change of just over 17%. This lesser increase implies that the average lean weight of juveniles must also have increased slightly during their first winter of life.

The patterns outlined above may now be related to different events in the annual cycle.

(a) During Moult

In most years, adult godwits do not return to Lindisfarne until late October, by which date they have almost finished moult of their primary feathers. For example, in 1970, a sample of birds collected on 1 November contained seven adults, all growing their outermost one or two primaries. In 1974, however, some adults returned to Lindisfarne unusually early and in full breeding plumage. By early September, some of these birds had almost finished wing moult, while others had renewed only half their primaries. (Chapman (1924) recorded the arrival in mid-August 1918 of adults in active wing-moult). The fat levels of moulting birds varied very little amongst individuals, or with date, throughout September and October. Similarly, the pectoral muscle indices varied very little in moulting birds and were not significantly different from those of non-moulting adults at other times of year. This suggests that there was no marked increase in body water, including blood volume, during moult, since this should have led to a lower muscle index when expressed as a proportion of any increase in body weight. Nor was there evidence of use of the pectoral muscles as a protein source for feather production, since this would have led to lower muscle indices, when expressed either as a proportion of lean body weight or in relation to skeletal size.

(b) During and after autumn migration

As mentioned above, in 1970 a sample of moulting adult godwits was collected on 1 November, within a few days of their arrival at Lindisfarne. These had a slightly, but not significantly, lower mean Lipid Index than moulting birds which had been at Lindisfarne for several months. This difference was attributable chiefly to one November bird with an index of only 2.7%, some two per cent below normal. After migration, the size of the pectoral muscles, measured in relation to skeletal size, was significantly lower ($p < 0.01$, t-test) than in the other moulting birds. However, when expressed as a percentage of lean weight, the muscle index of the post-migratory birds was not significantly lower. These observations are consistent with the idea that some muscle protein is used during the migratory flight, together with an approximately equivalent percentage of body water, so that the ratio of muscle weight to total lean body weight remains almost unchanged. Comparison of the October and 1 November data indicate an average loss of some 13% in the weight of the pectoral muscles. Much of this loss was made good by mid-November, as indicated by the significant rise in muscle index during that month.

In the case of juveniles, there is less certainty that individuals were collected very soon after arrival at Lindisfarne. Nevertheless, the September data show pectoral muscle weights low in relation to skeletal size, but average in relation to lean body weight, just as found in the adults. By October, several weeks after the arrival of most of the juveniles, their muscl weights had risen considerably. Two juveniles collected on 1 November had very high Lipid Indices (Fig. 4) similar to that (19.0%) of a juvenile held in captivity until mid-November. Presumably these birds would have migrated further. However, their muscle indices were lower than average.

(c) During winter

In most winters, godwit numbers at Lindisfarne remain steady from November to late January. The mean Lipid Indices of both adults and juveniles rise to a peak of about 12% in mid-December, when days are shortest, and decline thereafter as days lengthen. This lipid reserve can be used for either or both of two purposes: (i) to augment daily food intake when this is insufficient to meet daily maintenance costs (ii) to provide fuel for flights to other areas. At worst, when the intertidal zone is completely frozen, godwits are unable to feed. Under these conditions, the fat reserves carried in mid-December, totalling between 30 and 40 gms (depending on the size and sex of the bird) would be sufficient to provide maintenance energy for about three days.

In contrast, no protein reserve appears to be laid down, at least in the pectoral muscles, to guard against temporary starvation in mid-winter. In adults, the two muscle indices are no higher in mid-December than during moult, when, as argued above, they might have been expected to be low. In juveniles, also, the rate of increase in both muscle indices between autumn and spring appears to be steady, with no mid-winter peak.

(d) Before and during spring migration

Most godwits which winter at Lindisfarne leave the area by late April. However, others arrive to take their place, some stopping only briefly before continuing migration northwards, a few hundred immatures remaining throughout the summer. As judged by direct observation, the Lindisfarne wintering population contains more short-billed males than long-billed females. In the September to March samples collected for this study 56% of the birds were male, 44% female. By contrast, the sample of 13 one-year old birds collected on 8 May 1974 contained 70% females. This sample of passage migrant and/or potential summering birds contained only two individuals with fat levels sufficient to perform significant further migration. Possibly the rest had arrived only recently and so had not had time in which to prepare for further migration. Their Lipid Indices averaged only 3%, similar to the majority of juveniles in April. In both months the highest Lipid Indices recorded were 12-13%, comparable to mid-winter levels. No adults were examined in May; those collected in April had Lipid Indices averaging 6.5% and included no exceptionally fat individuals. Presumably the spring migration of godwits to Siberia takes place by a series of short flights from one refuelling area to another.

Both muscle indices of juvenile godwits reached their highest values in April and May. It might be supposed that this indicates growth of the pectoral muscles associated with preparation for migration, but this is not certain, since the muscle indices obtained were not significantly greater than those of adults in the following autumn. Furthermore, there was no statistically convincing evidence of muscle hypertrophy in adult godwits befor their migration in April, although the index relating muscle weight to skeleta size in adults reached its highest mean value of the year in that month.

(ii) Departures from the normal patterns of change: birds in "poor condition"

The inability of birds to maintain fat and muscle reserves at levels appropriate for the time of year must be the result of inadequate food intake. A number of possible situations can lead to this. Birds cannot feed during a migratory flight, may be unable to feed effectively during cold weather (for reasons to be discussed later) or may be injured.

It is well known that fat stored before migration is used as fuel during the flight; but little information is available on the levels of fat remaining at the end of the journey. Information presented earlier showed that only one of seven adults collected after arrival on 1 November 1970 had a Lipid Index notably below normal for the time of year. (One of nine juveniles collected on the same day had an equally low Lipid Index (2.6%), and possibly was a passage migrant.) These data suggest that the levels of fat accumulated before migration usually are more than sufficient for the flight, and allow a safety margin similar in quantity to the normal levels of fat carried by non-migrants at that time of year. By contrast, the muscle weights of adults after migration (measured against skeletal size) were lower in six of the seven birds examined than the lowest muscle weight recorded in non-migrants between September and early December. Using muscle as the criterion, therefore, most godwits were in "poor" condition after migration, even though they carried adequate fat reserves.

The effects of a period of cold weather in restricting food intake are exemplified by the changes in body composition of samples of godwits taken on 20 and 25 December 1970. The average Lipid Index of adults fell from 12.8 to 11.5%, a non-significant drop, as the variation in Lipid Index about the mean was wide on both days. The lowest fat levels recorded before and after the cold spell were 8.9 and 7.4% respectively. Thus, although apparently in poorer condition after five days of cold weather, adult godwits must have maintained daily energy intake almost at the levels needed to meet their daily requirements. Juveniles fared less well. At the end of the cold weather, their Lipid Indices averaged only 8.5%, significantly lower ($p = 0.05$ t-test) than those of adults collected on the same day. Three of the eight juveniles carried fat levels lower than that of the adult in "poorest condition". The juvenile with least fat (5.0%) had one tarsus which had been broken but had healed subsequently. Muscle weights, measured against lean body weight, showed no change during the cold spell. However, when measured against skeletal size, the pectoral muscles of the sample of adults collected on 25 December, after the cold weather, were lighter than those of the sample collected on 20 December. As in the fall in Lipid Index, the change was non-significant, since the variation in muscle index around the mean was wide on both days. One adult had an index as low as 0.246, similar to the lowest values recorded in the birds collected after migration on 1 November. The mean muscle index of juveniles collected on 25 December was very similar to that of the adults, but this value is based on only seven of the eight juveniles and omits one individual with an exceptionally low muscle index of 0.207. (This bird had a Lipid Index of 11.8%, well above average). Although this juvenile was in "poor condition", using the criterion of pectoral muscle weight, it should not be assumed that its chances of survival were very low, for its muscle index was identical with that of a healthy captive bird, in which the pectoral muscles had atrophied through disuse.

Exceptionally low fat levels for the time of year were obtained from two juvenile males in September /October 1974 and one adult male in March 1971. These birds had no noticeable deformities but were roosting or feeding singly. An adult male with a broken leg collected in early March 1971 also had an abnormally low Lipid Index. However, three other birds with bone damage which had healed - including one which had lost its right foot - had normal Lipid Indices, as did another carrying a heavy load of intestinal parasites. The muscle indices of the juveniles roosting alone were normal, but those of the adult males collected in March, while feeding solitarily, were very low.

It is not known why the solitary birds were feeding or roosting alone. We showed earlier (Smith and Evans 1973) that godwits feeding singly had lower rates of prey capture than birds feeding in flocks. This could lead to loss of condition. Alternatively, birds which develop poor condition may then leave the feeding flocks.

Discussion

(i) Are muscle and fat levels two independent criteria of condition?

Hanson (1962) argued that during migration, food shortage or starvation, fat can be utilized as an energy source only with concurrent breakdown of protein. Fat is metabolized via the Krebs' cycle, provided that a supply of oxaloacetate, which can be derived only from carbohydrate or protein metabolism, is also available. During starvation, a bird's carbohydrate reserves are exhausted quickly; therefore, Hanson claimed, protein must be the source of the oxaloacetate: "fat is burnt in the flame of protein". We see no reason, however, why oxaloacetate, once provided, should be used up during fat catabolism, since it should be reformed (without loss) during the working of the Krebs' cycle. Therefore we claim that protein breakdown is not necessary for fat utilization. However, all warm-blooded vertebrates have high rates of protein turnover in the liver and so require its continual intake. "The primary function of protein food is to supply the amino-acids needed for the growth, repair and general maintenance of the structural and catalytic machinery of living cells" (Baldwin 1967). Hence, during any period of inadequate protein intake, protein reserves within the body itself, e.g. the pectoral muscles (Kendall, Ward and Bacchus 1973), will be utilized to provide the necessary amino-acids. During starvation, resulting either from food becoming unavailable, or from prolonged continuous migratory flight, a bird's muscles are likely to be used as the source of protein at the same time as its fat reserves are used as an energy source. During times of merely shortage of food, however, a situation could arise in which the daily protein intake was adequate, but the total energy intake insufficient, to meet the daily requirements. Under these conditions, a bird's fat reserves would decrease, but no change would be expected in the weight of its muscles. With less favourable feeding opportunities, but not complete starvation, both fat and muscle reserves would be used up, but fat more quickly than protein. Under total and prolonged starvation, at least in man, the daily use of fat reserves remains steady, but protein reserves are drawn upon progressively less heavily as the duration of the fast lengthens, as a result of reductions in enzyme activities in the liver.

The conclusions to be drawn from the arguments outlined above are that fat and muscle levels are independent measures of condition, but that they often vary in parallel, though not necessarily to the same extent. Insofar as the data from adult godwits collected on 20 and 25 December 1970 are representative of the population as a whole, fat levels were 10% lower but muscle weights only 6% lower after the period of cold weather. This could be interpreted as indicating a level of difficulty in obtaining food which was sufficient to reduce both daily protein intake and, more particularly, daily energy intake below daily requirements.

(ii) Increases in muscle weight in birds: some general predictions

As mentioned earlier, restriction of daily food intake will not necessarily lead to the depletion of protein reserves in a bird's body, whereas even temporary starvation must do so. One may predict, therefore, that those species which are likely to meet conditions in which food is made unavailable for several days, during predictable periods of the year when e.g. droughts or snow cover are likely to occur, will increase their protein reserves in anticipation. In contrast, those species which usually encounter merely reductions in food availability at certain times of year, but rarely complete absence of food, may well not increase their reserves in anticipation Shorebirds, feeding in the intertidal zone which rarely freezes for more than a few hours in normal British winters, would be expected to fall into the second category, and it will be noted that adult Bar-tailed Godwits did not increase their muscle levels in anticipation of cold weather in mid-winter at Lindisfarne.

With regard to migrants, most of which cannot feed on the wing, the use of body protein must increase approximately in proportion to the duration of non-stop flight. If the food types and availability at the destination do not permit rapid replacement of lost protein by a migrant species, then one may expect that species to prepare for migration by muscle hypertrophy before departure. The longer the flight to unfavourable feeding areas, the greater the extent of hypertrophy to be expected. If, on the other hand, migrants are travelling only short distances or to areas where feeding conditions are good, then hypertrophy need not occur. In the Bar-tailed Godwits at Lindisfarne, any increase in muscle weight which may have taken place before autumn migration was insufficient to provide the protein needed during the flight itself. Hence, on arrival in early November, birds had pectoral muscle weights below normal; but feeding conditions normall are good at that time of year and the losses were soon made up. In spring, pre-migratory fat deposits were relatively small, and the apparent (but not significant) increase in muscle weight was also small. Presumably, the flight to the breeding grounds was not made directly from Lindisfarne, so the need for increased protein reserves before departure was lacking. It should be noted that small and medium-sized migrants do not need to acquire larger muscles to carry the extra fuel load during migration (Pennycuick 1969).

Hypertrophy of the pectoral muscles before migration, and a reduction in muscle weight during migration, has been claimed for several passerine species, e.g. the Lesser Redpoll Carduelis flammea leaving Britain in autumn (Evans 1969a) and the Yellow Wagtail Motacilla flava prior to crossing the Sahara while on northward migration in spring (Fry, Ferguson-Lees and Dowsett 1972), though in neither case was it proven conclusively that the fattest birds, which had the highest pectoral muscle weights, were not merely the largest birds in terms of skeletal size.

(iii) The functions and control of winter fattening in godwits

The peak Lipid Index in godwits occurred in December, when days are shortest, rather than one month later, when the average daily temperature tends to be lowest. This suggests that increased fat reserves may be an adaptation to restricted hours of daylight feeding, as well as to increased metabolic needs at lower temperatures. Although godwits can feed by night as well as by day, they are more successful by day, when they hunt primarily by sight. Their preferred prey occur chiefly below mid-tidal level and so are available for less than 8 hours in every tidal cycle. When high tides occur in the middle of the day in mid-December, godwits at Lindisfarne are able to feed on their preferred prey for no more than three hours during daylight. By mid-January, with similar tidal conditions, the natural increase of daylength allows them another half-hour of daylight feeding, so it may be argued that they do not need to maintain such large fat reserves then to cope with any sudden onset of adverse conditions. Many wader species studied on the Wash also reach peak weights (and therefore very probably peak fatness) in December rather than January, as may be deduced from data summarized by Minton (1973). In contrast, several passerines, e.g. the Yellow Bunting Emberiza citrinella, reach peak fatness in mid-January (Evans 1969b).

Unlike the winter fat deposits of passerines, those of godwits (and Oystercatchers Haematopus ostralegus (Dare, in prep.)) form a layer over the pectoral muscles, rather than being concentrated in the "tracheal pit" (between the clavicles) and over the peritoneum. Hence winter fat in godwits may serve an insulative function, as well as acting as an energy reserve to be drawn upon if daily energy intake falls below requirements, or for hard-weather movements. If the distributions of winter and pre-migratory fat in waders are similar, problems might arise in dissipation of the heat produced by the pectoral muscles during migratory flights. It has been argued that passerine migrants used air-cooled "engines" (Hart and Berger 1972), so additional insulation over the pectoral muscles would seem a disadvantage. However, in godwits, presumed pre-migratory fat deposition in April and May was less extensive than in mid-winter, so that the muscles were rarely overlain by a thick layer of fat.

While the adaptive nature of winter fattening in godwits seems clear, its proximate control is unknown. Several passerines, e.g. the White-crowned Sparrow Zonotrichia leucophrys and the Bullfinch Pyrrhula pyrrhula, respond to sudden cold weather by increasing their fat reserves immediately (King and Farner 1966, Newton 1969). However, the Yellow Bunting does not. The level of its reserves are linked solely to the date and are unaffected by temperature (Evans 1969b). In contrast, the Bar-tailed Godwit was unable to maintain its reserves during cold weather, but otherwise carried fat reserves linked to the date (Fig. 4). These fat levels could have been regulated via an internal rhythm or by daylength. Differences in the proximate control of the fat reserve in waders and passerines are to be expected in view of the differences in its function. Passerines use fat as an overnight energy supply and to provide sufficient energy to enable them to fly from their roost to search for food next morning. Waders are able to feed by night, but their foods may be less available in cold weather, whereas those of granivorous passerines are unaffected by cold _per se_, though they may be made unavailable by snow cover.

(iv) _Body condition, food availability, and feeding behaviour_

The depressive effects of cold weather on body condition, as measured by fat and muscle indices, link neatly with data on the feeding behaviour of godwits at different temperatures x(Smith 1974 and in prep.). Their chief prey are Lugworms _Arenicola marina_, which they detect and capture when the worms back up their U-shaped burrows to defaecate. When mud temperatures fall below 3°C, Lugworms become progressively less active and the rate at which they are captured by godwits decreases. When mud temperatures fall below freezing point, godwits manage to take very few lugworms, and rely on finding other, smaller, polychaete worms. They then have difficulty in satisfying their daily food requirements - as happened, particularly to the juveniles, in late December 1970 - and their lipid reserves are drawn upon.

Lugworms are less readily available to godwits also during periods of high winds, which dry the surface of the sand and reduce the frequency of defaecation by the worms. Gales also prevent godwits from feeding successfully at the tide-edge, as _Arenicola_ casts are washed away as fast as they are formed (so depriving godwits of the cues they need to find the

x This is hardly a reference.

worms) and the water becomes turbid, thereby reducing visibility. In early autumn, godwits seem able to cope with this situation, provided that gales do not delay or prevent the ebbing tide from uncovering their preferred feeding areas. They obtain their daily food requirements by lengthening their period of feeding to compensate for lower rates of prey capture. Even juveniles manage to compensate in this way, for the average Lipid Index of the sample taken on 4 October 1974, after three days of northerly gales, was not significantly different from that of juveniles collected in September or later in October (means of 5.2 as against 4.8 and 4.9%, respectively). We have no information to indicate how seriously the onset of gales would aggravate an already bad feeding situation for godwits during cold weather in mid-winter, or during periods of midday high tides when daylight hours are short.

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Summary

Body compositions have been determined of 169 Bar-tailed Godwits Limosa lapponica, collected at different times of year, between 1970 and 1975, at Lindisfarne, Northumberland. Normal trends in lipid and muscle indices are shown in Fig. 4. The lipid index (weight of fat as a percentage of total body weight) of both adults and juveniles reaches a peak in December when day-light hours are shortest. Both muscle indices (lean dry weight of all the pectoral muscles (i) as a percentage of lean body weight (ii) in relation to skeletal size) remain unchanged in adults throughout the non-breeding season, but increase steadily in juveniles to reach adult levels by late winter. Slight hypertrophy of the pectoral muscles may occur before migration. Birds with lipid and/or muscle indices below normal for the time of year are considered to be in "poor condition"; recovery of condition may be rapid, for example in adult godwits arriving at Lindisfarne with depleted muscles after autumn migration. During cold weather, lipid reserves are used to augment daily food intake if this is insufficient to meet daily energy requirements. At maximum, fat reserves alone could supply about three days' energy needs. Muscle may also be drawn upon as a protein reserve. Juveniles lose condition more rapidly than adults when food becomes less readily available in cold weather. Differences in the temporal pattern and functions of winter fattening in waders and passerines are discussed. Some predictions are made as to the likelihood of accumulation of protein reserves in winter or before migration in different bird species.

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Appendix I : Lean body weights (gm) of Bar-tailed Godwits at Lindisfarne

Date Period		Juvenile Male	Adult Male	Juvenile Female	Adult Female
September	Mean	242	258	297	335
	S.E.	7.7	6.1	6.2	9.1
	n	8	6	4	6
4 October 1974	Mean	266	292	323	326
	S.E.	6.8	8.7	9.3	-
	n	7	3	3	1
17/23 October	Mean	277	263	305	329
	S.E.	11.0	0	17.6	12.7
	n	5	2	4	3
1 November 1970	Mean	251	266	309	315
	S.E.	9.9	6.0	10.0	5.5
	n	5	2	4	5
November	Mean	270	269	331	321
	S.E.	3.9	5.8	17.0	49.5
	n	4	5	4	2
10/11 December	Mean	-	293	335	342
	S.E.	-	8.9	-	-
	n	-	3	1	1
20 December 1970	Mean	245	262	-	308
	S.E.	-	9.4	-	13.2
	n	1	4	-	3
25 December 1970	Mean	245	262	303	318
	S.E.	15.2	7.6	12.3	2.5
	n	3	5	5	2
14/16 January 1975	Mean	301	277	309	336
	S.E.	21.1	11.0	14.5	17.1
	n	3	2	3	4

	Mean	256	-	304	288
late January/ February	S.E.	2.0	-	-	6.9
	n	2	-	1	4
	Mean	267	274	-	-
March	S.E.	10.4	0.7	-	-
	n	3	3	-	-
	Mean	272	279	308	304
April	S.E.	3.3	11.5	3.0	9.4
	n	3	3	2	3
	Mean	282	-	311	-
8 May 1974	S.E.	6.2	-	6.6	-
	n	4	-	9	-

Appendix II: Fat and muscle indices of Bar-tailed Godwits at Lindisfarne

Date Period		Lipid Index (% of total body weight)		Muscle Index (% of lean body weight)		Muscle Index (related to skeletal size)	
		Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
September	Mean	4.8	5.8	5.26	5.88	0.245	0.296
	S.E.	.88	.42	.150	.104	.0077	.0036
	n	12	12	12	12	12	12
4 October 1974	Mean	5.2	5.5	5.26	6.62	0.277	0.301
	S.E.	.59	.54	.074	.066	.0040	.0079
	n	10	4	10	4	10	4
17/23 October	Mean	4.9	5.2	5.34	5.82	0.275	0.301
	S.E.	.25	.48	.082	.092	.0072	.0049
	n	9	5	9	5	9	4
1 November 1970	Mean	10.3	4.7	5.44	5.54	0.259	0.261
	S.E.	1.78	.39	.130	.152	.0102	.0069
	n	9	7	8	7	7	7
November	Mean	9.4	9.3	5.26	5.52	0.261	0.287
	S.E.	0.81	1.25	.096	.082	0.0086	.0055
	n	7	7	6	7	7	8
10/11 December	Mean	11.0	11.3	4.22	5.40	0.242	0.293
	S.E.	-	1.38	-	.108	-	.0079
	n	1	3	1	4	1	4
10/11 December	Mean	11.0	11.3	4.22	5.40	0.242	0.293
	S.E.	-	1.38	-	.108	-	.0079
	n	1	3	1	4	1	4
20 December 1970	Mean	12.2	12.8	6.30	5.76	0.280	0.292
	S.E.	-	1.11	-	.086	-	.0099
	n	1	7	1	7	1	7

25 December 1970	Mean	8.5	11.5	5.54	5.84	0.277	0.275
	S.E.	1.03	1.13	.118	.114	.0142	.0062
	n	8	7	8	7	7	7
mid-January	Mean	8.0	10.8	5.84	5.70	0.294	0.290
	S.E.	0.93	1.09	.136	.110	0.0101	.0081
	n	6	8	6	8	6	7
February	Mean	8.4	8.6	5.66	5.86	0.254	0.256
	S.E.	1.02	1.40	.118	0.34	0.0024	-
	n	3	2	3	2	3	1
March	Mean	-	-	5.76	-	0.300	-
	S.E.	-	-	-	-	.0027	-
	n	-	-	2	-	3	-
April	Mean	3.3	6.5	6.16	5.84	0.326	0.309
	S.E.	0.27	0.76	.116	.232	.0141	.0130
	n	3	6	5	6	5	6
8 May 1974	Mean	3.0	-	6.12	-	0.311	-
	S.E.	0.21	-	.134	-	.0090	-
	n	9	-	13	-	13	-